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SOUTH AFRICAN MUSEUM

VOLUME XXXI.

DESCRIPTIONS OF THE PALAEONTOLOGICAL MATERIAL COLLECTED BY THE SOUTH AFRICAN MUSEUM AND THE GEOLOGICAL SURVEY OF SOUTH AFRICA.

PART IV, *containing:*—

10. *A Critical Revision of the Quaternary Perissodactyla of Southern Africa.*—By H. B. S. Cooke. (With 31 Text-figures.)

Title Page and Index to Volume XXXI.

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10. *A Critical Revision of the Quaternary Perissodactyla of Southern Africa* *.—By H. B. S. Cooke, M.A., D.Sc., F.G.S., F.R.Met.S., F.R.S.S.Afr.

(With 30 Text-figures.)

Introduction.

The study of fossil mammals in Southern Africa has been far from systematic and, with a few rare exceptions, writers have been more concerned with placing new species on record than with studying the fauna and revising our knowledge in the light of later discoveries. The first fossil mammal known to have been found in this region is the giant "*Bubalus*" *bainii*, whose horns and damaged skull were recovered in 1839 by the remarkable civil engineer and naturalist Andrew Geddes Bain from alluvial deposits of the Modder River, Orange Free State. The material was described only in 1891 by the British palaeontologist Seeley, and the next record of a fossil mammal appeared in 1906 when Dr. R. Beck described a mastodon tooth from the gravels of the Vaal River. In the following year another German scientist, Professor E. Fraas, gave a further account of this tooth and commented on other remains from the gravels. Also in 1907, the celebrated American palaeontologist Professor W. B. Scott described a collection of fossil mammals from the coast of Zululand. Two years later Dr. Robert Broom made the first of his long series of contributions to mammalian palaeontology in South Africa with his descriptions of a new antelope from alluvial deposits at Caledon and of a new giant horse from a limestone fragment washed up on the beach near Maitland, in the south-western Cape. In 1913 Broom described an assemblage of mammalian fossils from the thermal springs at Floris Bad, and in later years he described several new mammals from the Vaal River gravels and various open sites.

In the past twenty-five years the initiative in the description of South African material has passed from the hands of outside experts like Seeley, Scott and Fraas to those of local workers such as Broom,

* Manuscript submitted in January 1946. Appendix added in October 1950.

Haughton, Dart, van Hoepen, Middleton Shaw and others. During this period a considerable body of material has been collected, but much of it has remained largely unstudied and undescribed unless something obviously new was noticed by the individuals through whose hands it passed. Even then it has been for the most part only the new genera and species which were described, and the fauna as a whole has received little attention. Van Hoepen has large collections from his site at Cornelia which still await description, the South African Museum at Cape Town and the McGregor Museum at Kimberley have hundreds of specimens collected over a long period, and other museums have smaller quantities of undescribed material. Since its inception in 1934 the Archaeological Survey of the Union has acquired notable collections as a result of the activities of several collectors, and little of this material has been described or considered as a whole.

During the years 1935–36 a joint survey of the Vaal River basin was carried out by Messrs. P. G. Söhnge and D. J. L. Visser of the Union Geological Survey, and Professor C. van Riet Lowe, Director of the Archaeological Survey, and during the survey much fossil material was recovered from various horizons in the deposits. The results of the geological and archaeological investigations were published in 1937, under the title "The Geology and Archaeology of the Vaal River Basin", as Memoir No. 35 of the Union Geological Survey, and it was intimated in the letter of transmittal of this Memoir that the fossil material collected would be described at a later date. Through the courtesy of the Director of the Geological Survey all this material was placed in the hands of the present writer for examination and report.*

It soon became apparent that a description merely of the material comprising this collection would be of little value, since it would not include all the species recorded from the deposits, and also because there occur in Pleistocene deposits other than those of the Vaal River basin many species which are likely at any time to be found within this area. For example, a tooth found at Christiana by a student and brought to the writer while this account was in course of preparation has been identified as belonging to a species hitherto recorded only at Cornelia in the Orange Free State. It was also only too obvious that the study of our fossil mammals had been far from systematic and that, with the notable exceptions of Haughton and Shaw, writers had been concerned more with placing new fossils on record than with comparative studies and revision of our knowledge in the light of

* See Appendix.

further discoveries. There exists a very considerable confusion of nomenclature and a multiplicity of specific names which renders the task of description of additional material virtually impossible unless it is accompanied by an amount of concurrent specific revision which would obscure the value of any account of the faunal assemblages. Indeed, it appears that until the material already described has been reviewed and new assessments made of the described species, it is of little value to proceed with the many other problems which our fauna presents.

In the course of his investigations on the cave deposits, Broom has to a certain extent reviewed and revised the Primates, Insectivora, Rodentia and Carnivora. Furthermore, these orders furnish the bulk of the cave fauna, and are virtually unrepresented in the material from open sites. Most of the fossils recovered from the Vaal River basin, surface deposits and other open sites belong to the Perissodactyla, Proboscidea and Artiodactyla. It has accordingly been decided that before the undescribed material can profitably be dealt with, the described species of each of these three important orders of mammals in Southern Africa must be critically reviewed. The present paper considers the first, and perhaps the most important, of these orders.*

As much as possible of the material from the Vaal River basin and elsewhere in the possession of the various museums in Southern Africa has been obtained on loan and examined in addition to the large collection in the Archaeological Survey. Dr. Broom has also been kind enough to make his material available to the writer. With the exception of those specimens which are in other countries, the type specimens of every species have been studied and are figured in the present account. Many of these figures have been drawn by the writer from the original specimens where the published figures are considered inadequate or unsuitable; others are reproductions of the original figures. As far as is possible new fossil material has deliberately not been introduced in this paper, as the purpose is to revise the specific descriptions from type material or from such other specimens as can with reasonable certainty be identified with the types. These descriptions are for the most part new, and are based on a fresh assessment of the original specimens interpreted in relation to the wider assortment of material now available and considered against a background of comparative researches upon the characteristics and variability of related living forms. It is hoped that this revision and

* See Appendix.

correlation of scattered data may help to place our knowledge of these fossil mammals in Southern Africa on a firmer basis than has hitherto been the case, and serve to evaluate the characters of the revised species in a form which may facilitate future identification and comparison.

Material.

As a result of the conditions which prevailed in Southern Africa in the Quaternary, the fossil remains which have survived are mainly teeth, though skull fragments, loose bones and horn cores are sometimes found under suitable circumstances. Almost all the described fossil mammalian species from this region have been named on teeth, and in the present account the descriptions of species generally give only their dental characters. Complete skulls are so rare that they need not be considered, and the identification of isolated bones is not yet possible, largely owing to the complete absence of whole or even partial fossil skeletons.

The majority of the published descriptions have been rather unsystematic and often scanty. It has therefore been considered generally advisable not to quote the original account but to use it and the specimens in the preparation of a new description. Where quotations are given, however, the quoted material is indicated by the usual signs. The type specimens of each extinct species are figured and, in the descriptions given in the text, it has accordingly been possible to give an account of the features of the *species* which may be used for identification rather than a mere list of the characteristics of the *particular specimen* or specimens. An attempt has also been made here to give a definition of the generic characters of any extinct genus which has not been defined by its founder separately from the description of the genotype species. Where the genus is represented only by a single species, or perhaps by two species, this generic definition obviously may require considerable future revision, but some care has been taken to select as generic characters only the most outstanding features which differentiate the material from related types.

The synonymy given for each species is as full as possible and, it is hoped, includes reference to all the specific designations given to fossil representatives of each described species. In the case of living species, however, the synonymy gives the reference to the type description only, and the further synonymy of the living forms can

be found in the ordinary zoological sources: * the names applied to petrified specimens now assigned to these living forms are, however, given as fully as possible. The accepted specific names of all species living within historic times are followed by an asterisk, to avoid their confusion with species extinct prior to historic times and known only as fossils.

In the descriptions of dental characters the nomenclature of the Cope-Osborn scheme has been followed as far as possible, in accordance with the generally accepted information available. Since there appears, however, to be some lack of uniformity in the conclusions regarding the homologies of the cusps, and there is occasionally some doubt regarding the application of certain terms, the terms applied in the present account are shown in a diagram of a typical member of each family described, or are clearly defined in the text.

For convenience and brevity the customary abbreviations are used to denote molar, premolar, canine and incisor teeth. Milk teeth are, on the whole, of little value for specific identification owing to their considerable variability and the uncertainty of the relationship between their characters and those of the permanent dentition. They are accordingly considered only when absolutely necessary.

In some cases a species is regarded as unrecognisable owing to the inadequacy of the material upon which it is founded or defined, and thus becomes a *species insuff. descr. aut inquirenda*. It may nevertheless be the case that a specimen which has been regarded as in itself inadequate for the creation of a species may be capable of reference to more adequate material.

The numbers assigned by the various museums to the type and other specimens mentioned in this text are given wherever possible, together with an abbreviation indicating the museum concerned, viz.:

Arch. Sur.	Archaeological Survey, University of the Witwatersrand, Johannesburg.
Dept. Anat.	Department of Anatomy, Medical School, University of the Witwatersrand, Johannesburg.
M.M.K.	McGregor Memorial Museum, Kimberley.
Nas. Mus.	Nasionale Museum, Bloemfontein.
S.A. Mus.	South African Museum, Cape Town.
Tvl. Mus.	Transvaal Museum, Pretoria.

* The most up-to-date synonymy is that given in "A Checklist of African Mammals", by G. M. Allen, Bull. Mus. Comp. Zool. Harvard, vol. lxxxiii, 1939.

ORDER PERISSODACTYLA.

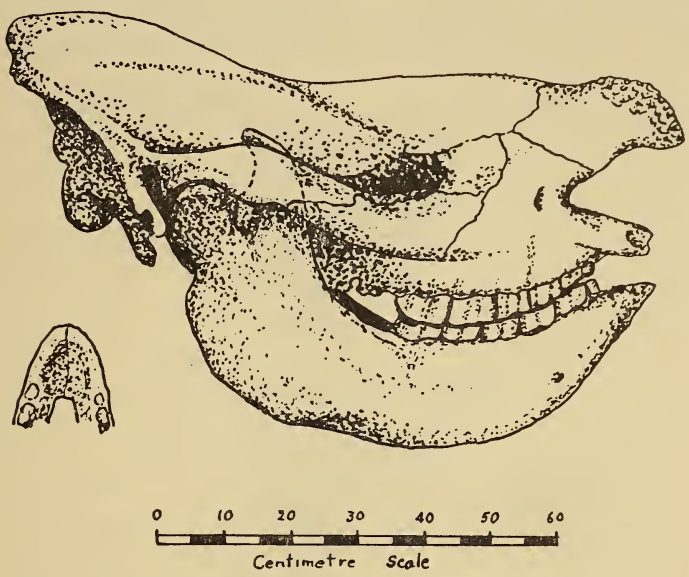
The Rhinoceroses.

Amongst the fossil mammalia, the rhinoceroses are only very scantily represented in Southern Africa. Two supposedly extinct forms have been mentioned, each only from a single site, but petrified specimens indistinguishable from the two living species have been recovered from various superficial deposits. These latter specimens are probably not of any very great antiquity, but rhinoceros species are in any case not subject to rapid changes.

The two living forms belong to different genera, and both their skulls and their teeth are quite distinct. The square-lipped or white rhinoceros is quite considerably larger than the hook-lipped or black rhinoceros, as can be seen from the drawings of their respective skulls (fig. 1). The lower jaws are sharply distinguished, that of the black rhinoceros having a deep compressed symphysis as compared with the depressed and rather spatulate symphysial region of the mandible in the white rhinoceros. The horns have been found isolated and again differ widely in form. Incisor and canine teeth are rudimentary or absent in both species.

The cheek teeth in the rhinoceroses comprise four premolars and three molars arranged in a continuous series and having essentially the same structure, though the first premolar is considerably more simplified and is shed early. The lower third molar is also simple, and does not possess the third lobe so characteristic of the horses and most artiodactyls. The premolars are somewhat smaller than the true molars, the second premolar and first premolar particularly being smaller than the more uniform succeeding teeth. Structurally the teeth differ from those of the horse in being rather low crowned and in possessing strong, distinct roots, but their essential composition is similar to that of the equine cheek teeth. The normal order of eruption of the permanent dentition appears to be M^1, Pm^1, Pm^2, M^2, Pm^3, Pm^4, and lastly M^3, and is thus somewhat different from that of the horses.

The cheek teeth of the rhinoceroses are lophodont in form, *i.e.* the rows of cusps tend to become fused into ridges. In the upper teeth the two main outer cusps form a ridge known as the *ectoloph*, two anterior cusps form the *protoloph* and two posterior ones the *metaloph*. In the lower teeth three triangularly arranged cusps unite to form a crescentic *metalophid*, and posterior to this two cusps form an arcuate



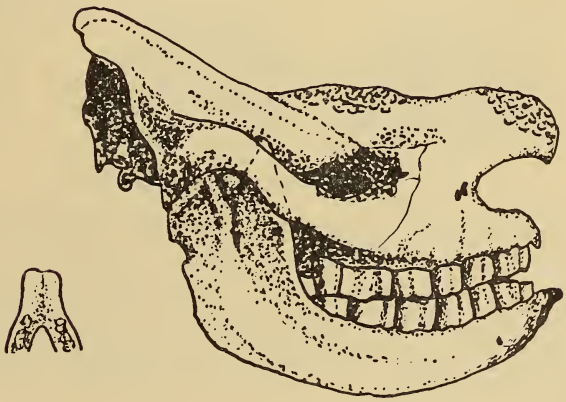


Fig. 1.

Above: Lateral view of skull of *Ceratotherium simum** (Burchell) and plan view of spatulate symphysial region of the lower jaw. (After Sclater.)

Below: Lateral view of skull of *Diceros bicornis** (Linnaeus) and plan view of the compressed symphysial region of the lower jaw. (After Owen.)

hypolophid ridge. With wear the enamel is rapidly removed from the top of these ridges and an area of dentine surrounded by enamel is exposed. This can be clearly seen in fig. 2, in which typical upper and

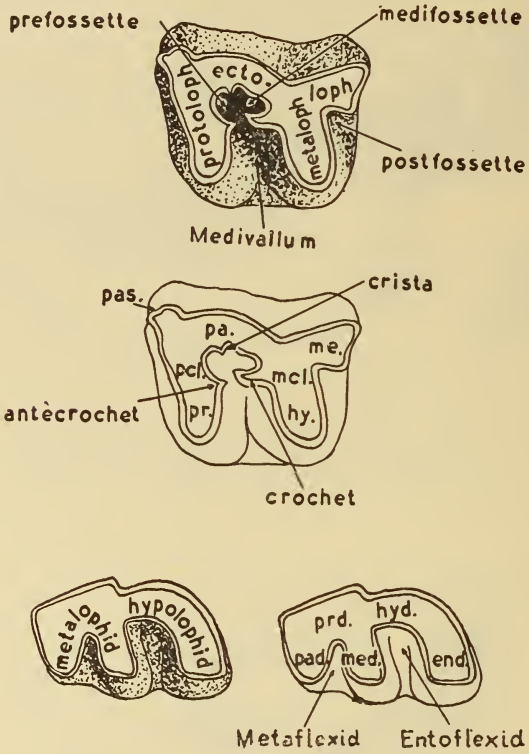


Fig. 2.—Molar elements (following Osborn) of the upper and lower cheek teeth of the Rhinoceros group.

Abbreviations.

Upper teeth: *pas*, parastyle; *pa*, paracone; *me*, metacone; *hy*, hypocone; *pr*, protocone; *pcl*, protoconule; *mcl*, metaconule.

Lower teeth: *prd*, protoconid; *hyd*, hypoconid; *pad*, parastylid; *med*, metaconid; *end*, entaconid. (Original.)

lower first molars are shown indicating the nomenclature used for the cusps, folds and ridges (following Osborn). The valley between the protoloph and metaloph appears to have received no name, and is here termed the medivallum by analogy with the corresponding valley in horse teeth. For the two inlets in the lower teeth the terms "metaflexid" and "entoflexid" are here suggested for convenience

in description, as the same terms have been proposed by Stirton (1941) in the lower teeth of the horses.

Owing largely to a lack of sufficient material, it has unfortunately not been possible to gain any reliable idea as to the constancy or variability of the tooth characters within the series in the rhinoceroses. From the limited material examined, however, it does appear that while the essential structures are reasonably constant, the effect of attrition alters the pattern of the grinding surface to such a degree that identification may be made most difficult. As wear proceeds, the ridges widen and obliterate the intervening valleys, at first fairly slowly, but afterwards very rapidly, until ultimately a uniform tract of dentine may be produced. The crochet, antecrochet and crista which project into the medivallum are generally more prominent in early wear, and are reduced in size as this valley is narrowed. In some species the crochet and crista may unite and isolate the medifossette as an accessory valley, leaving the prefossette as the terminal portion of the medivallum. The postfossette may also become isolated by closure of the posterior enamel border. In the lower teeth the chief effect of attrition is to reduce the size of the two flexids, the metaflexid in particular tending to disappear with wear. Fusion of the metaconid and entaconid may also lead to the complete isolation of the entoflexid as an accessory valley.

Family RHINOCEROTIDAE.

Genus Diceros Gray 1821.

Genotype: *Rhinoceros bicornis** Linnaeus.

*Diceros bicornis** (Linnaeus).

*Rhinoceros bicornis** Linnaeus 1758. Syst. Nat. Ed. (10), i, p. 56.
Opsiceros simplicidens (pars) Scott 1907. 3rd Rep. Geol. Surv. Natal and Zululand, pp. 258–259, pl. xvii, figs. 4, 5.
Diceros whitei (pars) Chubb 1907. Geol. Mag., V, vol. iv, pp. 447–448.

The horns of the black rhinoceros are almost invariably two in number, but exceptionally as many as five have been recorded. The anterior horn has a height of about forty-five to sixty centimetres on the average and has a basal diameter fifteen to twenty-five centimetres. The rear horn is about one-third to one-half the length of the anterior one and has a diameter only a little less than its height. The record horn lengths are about double the average figures. Both horns are rather blunt and curve very slightly posteriorly.

In the upper jaw the first premolar is very small and exhibits no

structures which can be said to be recognisable as persistent. The third molar is triangular in form, the metaloph, being reduced to a small posterior prominence only, and this tooth is very variable in pattern in wear and is of little value for specific identification. The remaining three premolar and two molar teeth are generally more consistent, and are essentially similar in structure, though the premolars differ slightly from the molars. In the premolars the anterior wall of the protoloph is fairly straight and makes an angle of about 75° with the ectoloph, whereas in the molars the protoloph initially makes almost a right angle with the ectoloph, and then curves somewhat posteriorly. The protoloph and metaloph are roughly parallel or slightly divergent and with the ectoloph give the appearance of the Greek letter π. The ectoloph itself is not straight, but has an outer wall incurved or grooved between the paracone and metacone and also has a shallow groove behind the parastyle. The parastyle itself is commonly anteriorly grooved and projects very little in front of the protoloph. The antecrochet is apparently absent, and the crista is very small and disappears rapidly with attrition. A crochet is always present in the earlier stages of wear, and in the normal dentition increases progressively in size from the second premolar to the second molar. It tends to become rounded with increased wear, and may disappear completely before the medivallum is obscured. In no case has isolation of the medifossette been observed in this species except in the third molar. The postfossette is somewhat obliquely V-shaped, tending to be U-shaped with wear as a result of the expansion of the hypocone lobe of the metaloph, and then becomes isolated as an oval valley. The dimensions vary considerably with wear, the breadth across the grinding surface increasing as attrition proceeds. The height above the basal cingulum increases progressively with the successive teeth, and a typical second molar in early wear has a height of about 50–55 mm. The breadth at the base of the second molar is about 60 mm., but in normal wear the grinding surface measures only some 45 mm. transversely. The size and characters can be seen from the scale drawings in fig. 3. Two typical upper dentitions are shown, one in fairly early wear, the other well worn and lacking the first premolar.

The lower teeth have little to distinguish them from the very generalised form of most rhinoceros teeth. The first premolar is greatly simplified in form, but the remaining teeth, including the third molar, are similar in structure. The anterior and antero-external walls of the metalophid are markedly flattened, and make an

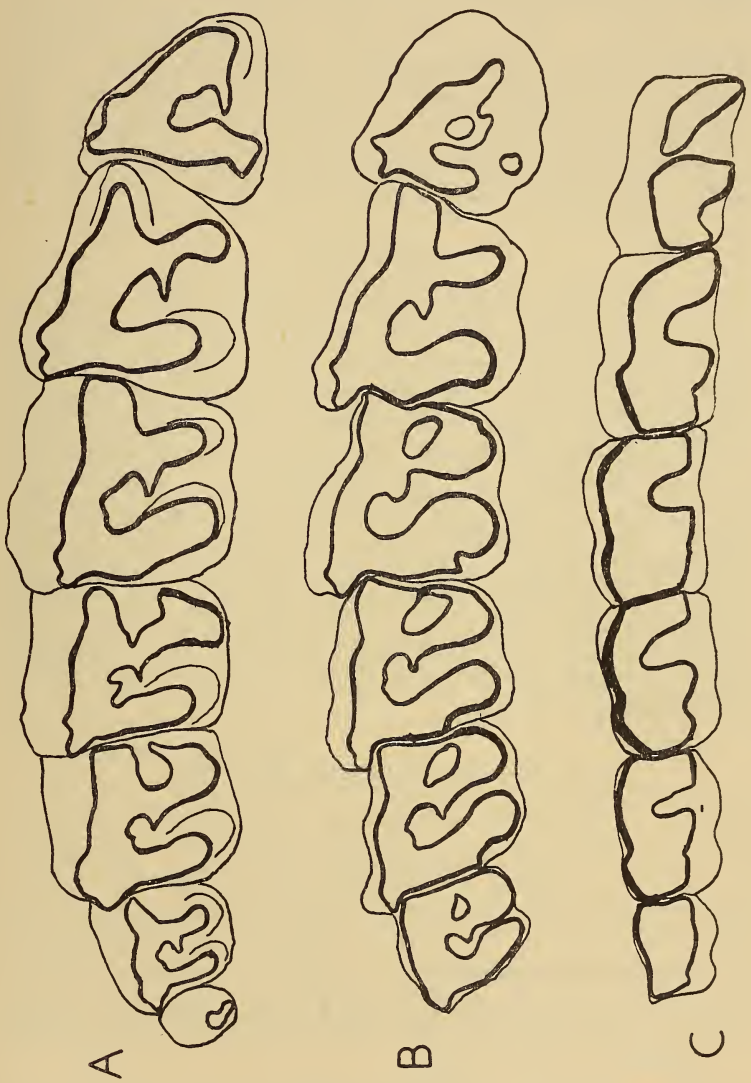


FIG. 3.—Two left upper dentitions (A and B) of *Diceros bicornis** (Linnaeus) and a right lower dentition (C) of the individual B. One-half natural size. (Original.)

angle with each other of about 100° or a little more. A fairly marked groove separates the outer wall of the metalophid from the curved hypolophid wall. The inner walls of the metaconid and entaconid are somewhat flattened. The metaflexid is a good deal smaller than the entoflexid and is rapidly reduced to a shallow V-shaped notch. The height of a normal second molar is about 50 mm. The lower teeth of a typical specimen are shown in fig. 3, and belong to the same individual as the upper dentition figured immediately above it.

Referred Material.

Apart from the petrified specimens from superficial deposits in various parts of Southern Africa which obviously belong to this species, two of the teeth from Zululand which Scott (1907) very tentatively referred to his species *Opsiceros simplicidens* do not appear to warrant distinction from the living *Diceros bicornis**. The type LM^2 of Scott's species manifestly is not that of *D. bicornis**, but the two heavily worn teeth (M^1 and Pm^4) do not differ appreciably from correspondingly worn teeth in old individuals of the living black rhinoceros. Scott himself realised the close similarity, and suggested that these two teeth did not actually belong to his new species. The specimens themselves have not been seen by the present writer, but natural size photographs kindly supplied to the writer by Professor Scott, together with the admirable description, form an adequate basis for the conclusion reached above.

Genus Ceratotherium Gray 1868.

Genotype: *Rhinoceros simus** Burchell.

*Ceratotherium simum** (Burchell).

*Rhinoceros simus** Burchell 1817. Bull. Sci. Soc. Phil. Paris, F. 1, 2, p. 97.

Opsiceros simplicidens Scott 1907. 3rd Rep. Geol. Surv. Natal and Zululand, pp. 257–258, pl. xvii, fig. 3.

Rhinoceros scotti Hopwood 1926. Occ. Papers No. 2, Geol. Survey, Uganda, pp. 16–17, fig. 3.

The white rhinoceros possesses a long and rather slender anterior horn which attains a height of about ninety centimetres and, exceptionally, as much as a hundred and fifty centimetres.* The second or rear

* Southern race: $62\frac{1}{4}$ inches. Rowland Ward's Records of Big Game, 9th ed., 1928, p. 446.

horn is small and does not usually attain a height exceeding twenty-five centimetres. The anterior horn is normally more slender than that of the black rhinoceros.

In the upper jaw the first premolar is small and is shed early, but the other premolars differ notably from the molars, for in the former the medivallum becomes rapidly enclosed by fusion of the protocone and hypocone, the form of the metaloph being consequently also affected. From *Diceros bicornis** they differ most markedly in the arcuate, posteriorly curving protoloph, and in the early fusion of the well-developed crista with the crochet to form an isolated medifossette. Due to the posterior curving of both protoloph and metaloph the π-like shape of the teeth is very distorted and not nearly as noticeable as in *D. bicornis**. The form of the ectoloph is also different, being rather more undulate in *Ceratotherium simum** with a distinct outward bulge at the paracone. The parastyle is more pointed and is not apparently grooved, but there is a groove immediately behind it. The postfossette becomes isolated with wear as a result of closure of the posterior enamel. As in *D. bicornis** this isolation of the postfossette is not a constant feature and is generally less marked in the molars than in the premolars. The teeth are higher crowned than those of the black rhinoceros, a typical second molar in normal wear measuring about 75 mm. above the indistinct cingulum. Fig. 4 shows (half natural size) two upper dentitions, one in very early wear with the third molar only just erupting and the fourth premolar coming into use, the second dentition being in a more advanced state of attrition.

The lower teeth are somewhat difficult to distinguish from those of the black rhinoceros. The anterior and antero-external walls of the metalophid make an angle with each other close to 90° instead of the obtuse angle found in *D. bicornis**. The metaflexid appears to be more persistent in the white rhinoceros than in the black, and the enclosure of both metaflexid and entoflexid with advanced wear is a common feature. The height of a typical second molar above the cingulum is about 60 mm. The lower dentition of the same individual as the more worn upper dentition figured is shown in fig. 4.

Referred Material.

Petrified specimens of this species have been found in various superficial deposits in the coastal region and in the interior. A portion of an anterior horn is also recorded from a cave deposit near Kuruman, Cape Province (Malan and Cooke, 1941).

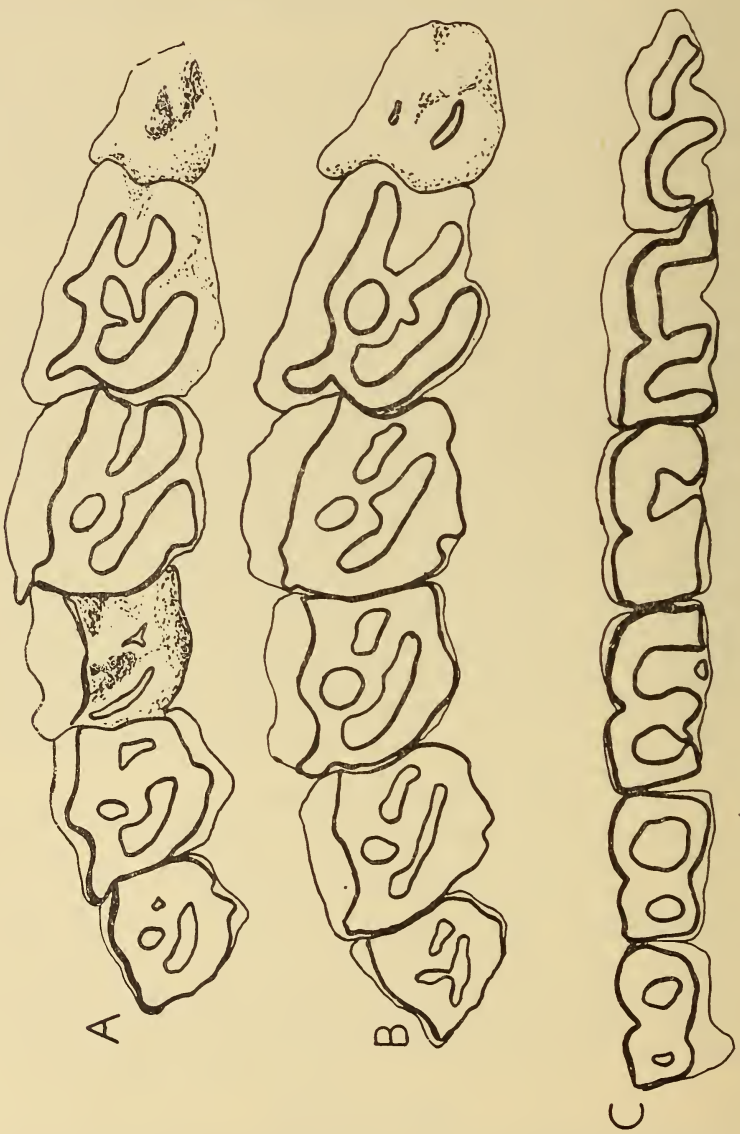


Fig. 4.—Two left upper dentitions (A and B) of *Ceratotherium simum** (Burchell) and a lower right dentition (C) of the individual B. One-half natural size. (Original.)

W. B. Scott reported in 1907 the discovery of a supposedly extinct species in fossiliferous marine clays from the Zululand coast, and he named this species *Opsiceros simplicidens*, with an unworn upper left second molar as the type. Scott compares this tooth with the corresponding one of *Diceros bicornis**, and states that the differences are "clearly of specific value". The distinctive characters are stated to lie, *inter alia*, in the much stronger recurving of the protoloph and in the much better development of the crista, which "fuses with the anticrochet so as to enclose a small and apparently shallow fossette". (Scott here used the term 'anticrochet' in error for crochet, as his figure shows, and in this follows an error previously made by Osborn in describing the Perissodactyla of White River (Scott and Osborn, 1890).) The characters which Scott used to differentiate the species from *D. bicornis** are exactly those which distinguish the white rhinoceros. A skull of the latter species in the South African Museum possesses a second molar in much the same state of development, and the dimensions and appearance of this tooth correspond very closely to the data and figure furnished by Scott. There can thus be little doubt that *Opsiceros simplicidens* is a synonym of *Ceratotherium simum**, a fact which Scott would undoubtedly have realised had comparative material of this rather rare species been available to him.

In 1926 Hopwood recorded an upper left second molar from the Kaiso beds of Uganda and assigned this specimen to Scott's species. He also pointed out that the name *R. simplicidens* was preoccupied and proposed *Rhinoceros scotti* as a substitute. There seems no doubt of the correctness of the reference of this specimen, and equally there is little doubt of its similarity to teeth of the living white rhinoceros. *Rhinoceros scotti* is thus also apparently a synonym of *Ceratotherium simum**.

Discarded Species.

Diceros whitei Chubb.

Diceros whitei Chubb 1907. Geol. Mag., V, vol. iv, pp. 447–448.
Diceros whitei Hopwood 1928. Rhodesian Man and Associated Remains.

A supposedly new species of rhinoceros was described very briefly by E. C. Chubb in 1907 in a "List of Vertebrate Remains" from the Broken Hill Cave. It was founded on two limb bones (a right tibia and a right humerus) which had been excavated by Mr. Franklin

White and presented by him to the Rhodesian Museum. This species was also mentioned by A. T. Hopwood in the British Museum memoir on Rhodesian Man, and is there said to be "closely allied to *D. simus*". In view of the uncertainty of the generic position of the species *whitei*, the material was obtained on loan from the Rhodesian Museum, Bulawayo, and permission was obtained from Mr. Chubb to amplify his preliminary description and to figure the specimens. In his brief account Chubb remarks on the scantiness of the comparative material available to him, and this lack and the seeming association of the two bones appears to have resulted in an error in the distinction of the material. The tibia is certainly that of a rhinoceros, though comparison with recent skeletons shows no notable differences in size or in other characters from the corresponding bone in the living *Diceros bicornis**. The humerus, however, differs very considerably from both the living rhinoceroses, and it would appear that it is an artiodactyl and not a perissodactyl humerus, the differences formerly regarded by Chubb as of specific distinctness being actually too great for that possibility to be upheld. The compressed narrow olecranon fossa is a normal artiodactyl feature unlikely to occur in a rhinoceros, and the deltoid ridge and deltoid tuberosity are also much more artiodactyl than perissodactyl. With these views Mr. Chubb now expresses his agreement.

On comparison with various living artiodactyls, the closest resemblance is found between the fossil humerus and that of the living Cape Buffalo. There is no great difference in length, but the fossil bone is somewhat more massive, with the attendant minor modifications consequent upon its greater weight-supporting requirements. Otherwise, however, there is a very close agreement in every character, and it seems highly probable that the fossil humerus belongs to a member of the Buffalo group. It may possibly belong to the extinct "*Bubalus*" *bainii* Seeley, or to "*Bubalus*" *andersoni* Scott.

The species *Diceros whitei* appears, therefore, to have been founded on a humerus which is not that of a rhinoceros and on a tibia which does not warrant distinction from the living *D. bicornis**, so that *D. whitei* must be regarded as incorrectly founded.

The Horses.

There have been described at various times from Southern Africa more than twenty-five species belonging to this family, some based on upper and some on lower teeth, but of these not more than half can be

regarded as valid. The position was first reviewed by Haughton in 1931 when the twenty then existing species were reduced to eleven, and in general the present writer is in agreement with these conclusions. Haughton divided the members ascribed to the genus *Equus* into two groups, which he terms the "quagga" group and the "zebra" group on the parallelism of certain characters with those in the teeth of the two living species, the bontequagga and the mountain zebra. Unfortunately these characters in the recently extinct true quagga are very different from those in the living bontequagga and the two group terms must therefore be abandoned.

The relationships indicated by Haughton's work are of great interest and, in order the better to appreciate the definitive characters of the teeth in the extinct forms, the writer has carried out an extensive examination of skulls and teeth of the living forms and of the recently extinct true quagga. As a result of this work it is possible to distinguish on dental characters from this material three undoubted species: *Equus zebra**, the living mountain zebra, *Equus quagga**, the recently extinct true quagga, and *Equus burchellii**, the living bontequagga or Burchell's zebra. Since zoologists have been greatly at variance on the status of these forms, and since all three species occur in the fossil state, the results of the investigation have already been considered fairly fully (Cooke, 1943). These observations also throw some light on the morphological characters and variations encountered in equine species and are of great value in considering the fossil finds. To some extent they repeat and amplify the work of Gidley (1901), and in the present examination a general agreement was found with the conclusions outlined by him.

For convenience of reference the nomenclature of the important elements of the molar teeth of the Equidae (following Osborn) is given here in diagrammatic form (fig. 5). The specimens figured are upper and lower fourth premolars, and show the appearance of the cusps on the unworn crowns and the enamel patterns of the teeth in normal wear. The two enamel islands in the upper cheek teeth have long been known as the pre- and postfossettes, but the partial islands, or inlets, in the lower teeth have until recently received no name. The terms advocated by Stirton (1941) are used here. They are respectively "metaflexid" for the anterior and "entoflexid" for the posterior partial islands of the lower cheek teeth. (These terms have already been suggested for the analogous parts of the rhinoceros teeth.) It is also proposed here to call the posterior groove which lies between the hypocone and the hypostyle in the upper teeth the "hypoglyph",

and the groove anterior to the protocone the "protoglyph". These terms are preferred to "hypoconal groove" and "preprotoconal groove" used by Stirton.

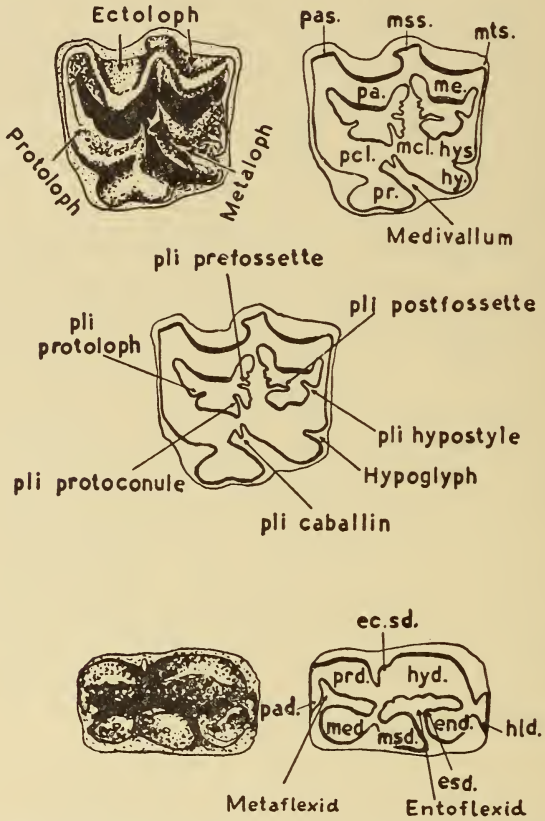


Fig. 5.—Molar elements (following Osborn) of the upper and lower cheek teeth of the Horse group.

Abbreviations.

Upper teeth: *pas*, parastyle; *mss*, mesostyle; *mts*, metastyle; *pa*, paracone; *me*, metacone; *hy*, hypocone; *pr*, protocone; *pcl*, protoconule; *mcl*, metaconule; *hys*, hypostyle.

Lower teeth: *prd*, protoconid; *hyd*, hypoconid; *med*, metaconid; *end*, entaconid; *pad*, parastylid; *msd*, metastylid; *hld*, hypoconnlid; *ec.sd.*, ectostylid (fold or ridge); *esd*, entostylid. (Original.)

Distinction between Zebra, Quagga and Bontequagga.

The writer has examined a large number of skulls of these three species in the past few years, though skulls of the recently extinct

quagga are rare and difficult to obtain. Owen (1869) figured one in a little known paper, there is a cast in the Transvaal Museum, one skull in the Kingwilliamstown Museum and several in the McGregor Museum, Kimberley. Based on an examination of this material the chief distinguishing features have been analysed (Cooke, 1943).

From the point of view of classification it would appear that the three species are quite distinct. The bontequagga or Burchell's zebra, while showing skull characters intermediate between the other two forms, is sharply distinguished in dental characters. There can thus be no doubt that the bontequagga is very distinct from the true zebra despite the many similarities of form and colouring which have caused much dispute amongst zoologists with respect to the relationship of the two forms. It differs to an equal degree from the true quagga, and can under no circumstances be regarded as a variety of this form. The specific designation *quagga** must therefore be restricted to the historically extinct true quagga, and the bontequagga or Burchell's zebra must receive the full specific name *burchellii**, to which may be appended, if it is considered necessary, the varietal names *wahlbergi**, *transvaalensis**, etc., though these varieties cannot be distinguished on skeletal or dental grounds as far as the present writer is aware.

The Degree of Constancy and Range of Variability of the Tooth Characters.

Aside from the examination of a large number of skulls of the zebrine group of horses to determine their distinctive features, an attempt has been made to estimate the range of variation found within each species and hence to estimate the value of each possible factor in specific determination. A number of skulls of *Equus caballus** and *Equus asinus** have also been used for this purpose, and reference has been made in addition to many published figures of equine dentitions to ascertain how widely the generalised conclusions may be applied. The factors appear from this examination to follow certain definite trends, a knowledge of which greatly enhances the value of the specific identification of individual finds of isolated teeth. It must be stated however that, despite this knowledge, a fossil species which is named purely on dental characters may well be a "form" species only, as there is a certain amount of overlap in the extreme variations of certain species. The first upper true molar of *Equus quagga**, for instance, may be almost identical with that of *Equus zebra** under certain conditions of variation.

One of the difficulties which besets the worker on the fossil Equidae is the fact that almost all the finds consist only of isolated teeth. Complete dentitions are very rare and are consequently of immense value. It is of the utmost importance therefore to ascertain correctly the position occupied by the isolated teeth in the former jaw in order correctly to evaluate the determinative characters. By far the most satisfactory method is that of direct comparison with a known complete dentition. The angle of wear and degree of antero-posterior curvature are the chief guides in the estimation as to whether a particular tooth is, for example, a fourth premolar or a first molar. Fig. 6 gives an indication of the general shape of the teeth in *Equus burchellii**, and figs. 6 and 19 show the form in some large extinct equines.

The second premolar is at once distinguishable by being rather pointed anteriorly, and the third molar shows a posterior tapering. The last erupted tooth of the series at any given age shows this posterior taper, however, so that in early wear such a tooth might possibly be a second or even a first molar. The rather sharp curvature of the true third molar should, however, facilitate the distinction of this tooth. In the lower teeth the premolars typically have a larger entoflexid than the molars, and the outer groove between hypoconid and protoconid extends further towards the inner groove between metaconid and metastylid in the true molars than it does in the premolars. In the upper teeth the first true molar normally has a rather narrow mesotyle, but otherwise the degree of curvature and angle of wear form the only guide to the position of the tooth in the series.

The factors which affect the characters of each cheek tooth in an individual of a species are: (A) The position of the tooth in the series, (B) the degree of attrition, and (C) variability within the species. The factor of sex does not appear to exert any appreciable influence on the cheek teeth, though the canines, which are usually prominent in the male, are vestigial or absent in the female. The generalised conclusions regarding the three main factors given above may therefore be discussed in turn.

A. The Position of the Tooth in the Series.

(a) *In the Upper Teeth.*

1. The anterior and posterior teeth (second premolar and third molar) show decidedly different forms of enamel pattern due to their tapering nature and are very variable in character. They are of the least possible value in specific determination, as the prefossette

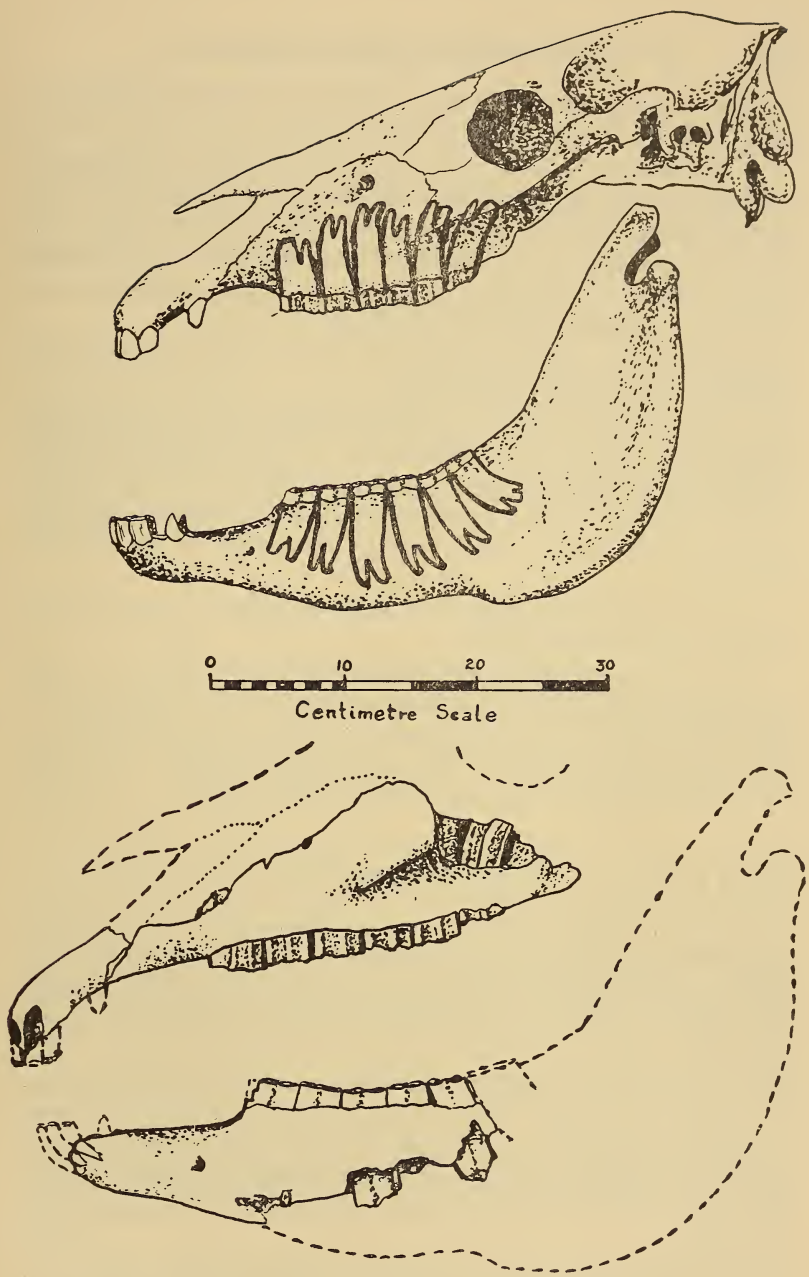


Fig. 6.

Above: Lateral view of skull of *Equus burchellii** (Gray) showing the shapes of the cheek teeth. (Original.)

Below: Lateral view of fragmentary remains of skulls of large extinct equines; Maxilla of *Equus fowleri* Wells, and mandible of *Equus plicatus* (van Hoepen). (Original.)

in the second premolar and the postfossette in the third molar are subject to considerable distortion.

2. In transverse breadth, measured from mesostyle to protocone, the third and fourth premolars are approximately equal, and the first and second molars usually slightly narrower (by perhaps 5–10 per cent.) than the preceding teeth. The second premolar and third molar are always narrower than the other premolar or molar teeth respectively, but bear no constant ratio of relative size.

3. The fourth premolar presents the most complex and the first molar the simplest enamel folding.*

4. The protocone is shortest (antero-posteriorly) in the second premolar and longest in the third molar. The length of the protocone either increases progressively in each succeeding tooth of the series or else the first molar has a smaller protocone than the fourth premolar, and the second molar has one about the same length as in the fourth premolar.

5. The mesostyle is generally reduced in width in the molars as compared with the premolars.

6. The pli-protoloph and pli-hypostyle may be lacking in the first molar though present in the remaining teeth.

7. The pli-caballin may be present in the premolars yet absent in the molars, and may occur in the fourth premolar only.

8. The hypoglyph is often absent in the third molar.

(b) *In the Lower Teeth.*

1. As in the upper teeth, the second premolar and third molar are of sub-triangular form and show departures from the normal enamel pattern. The changes are not always so great as to prevent specific identification, but they are the least useful teeth of the series for this purpose.

2. In transverse breadth the premolars are wider than the molars by about 5–10 per cent. The second premolar may, however, be as narrow as the first molar. The third molar bears no reliable ratio of width to the other molars, and in the second molar the posterior breadth is less than the anterior due to the reduction in size of the hypoconid.

* The normal order of eruption of the cheek teeth is M^1, M^2, Pm^2, Pm^3, Pm^4, and lastly M^3, though the order of the last two may exceptionally be reversed. In a normal dentition, therefore, the first molar in addition to possessing an initially less complex character is also the most worn tooth.

3. The entoflexid has a larger lobe in the premolars than in the molars, this being generally of greatest antero-posterior length in the second premolars.

4. The outer groove between protoconid and hypoconid is deeper in the molars than in the premolars and sometimes meets the internal groove between metaconid and metastylid.

(c) *Relation between Upper and Lower Teeth.*

Of great interest and value is the hitherto apparently unrecognised fact that the breadth over the enamel in the upper teeth bears a fairly constant ratio to the breadth of the lower teeth over the enamel. This ratio is approximately 1: 0·6 for the third and fourth premolars to 1: 0·55 for the first and second molars, and is apparently subject to a variation of only about 5 per cent.

B. The Degree of Attrition.

I. *Changes in Dimensions.*

The effects of the degree of wear (or age) on the cheek teeth have been well described by Gidley (1901), and the following selected quotations from his paper are illustrative of his findings in this regard.

1. "When a molar or premolar tooth first comes into use, the face, as well as the sides of the crown, is completely covered with enamel which folds in and out, and (though somewhat hidden by cement) presents the same general appearance as that seen in the much more primitive forms *Anchitherium* and *Mesohippus*. Soon the enamel on the tips of the cones and along the ectoloph wears through, and small patches and ridges of dentine surrounded by a border of enamel are exposed. As the tooth is further worn away, these patches and irregular ridges broaden and rapidly lengthen until when about one-half to three-quarters of an inch of the crown has been worn away they have all become united by narrow isthmuses, and the fundamental tooth pattern of the horse is presented." "From this point . . . the triturating surface presents a gradually less complex pattern of enamel folding as the tooth crown is worn away, until in the very much worn tooth the simplest pattern of enamel folding is presented" (fig. 7).

2. "The antero-posterior diameter of the first premolar (p_2)* remains about the same for the whole length of the crown, except that sometimes it narrows slightly near the roots."

* Actually the true second premolar according to present usage.

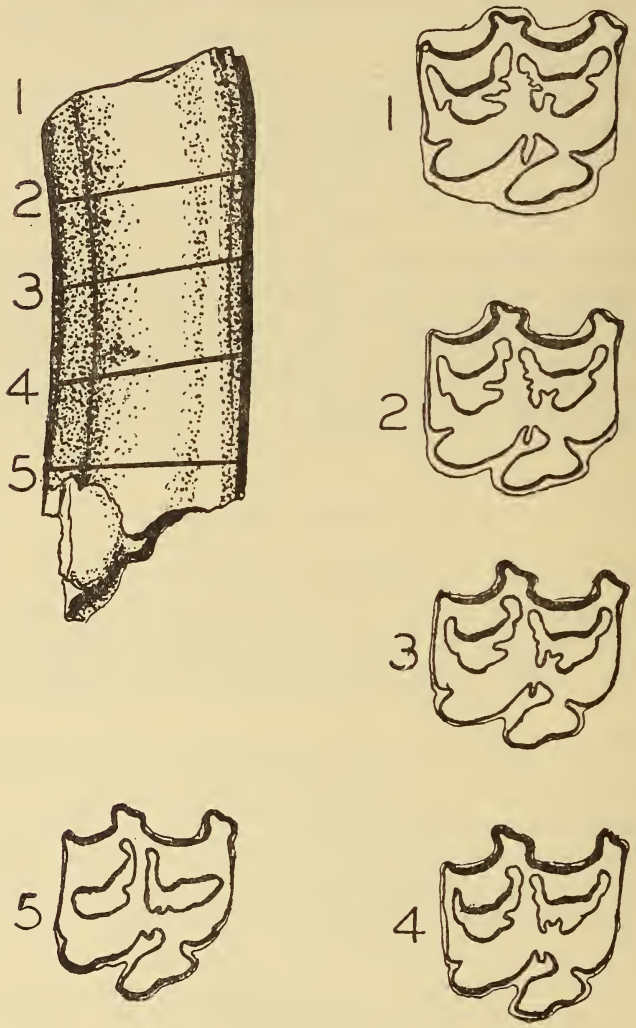


Fig. 7.—Sectioned right upper fourth premolar of adult male *Equus caballus** Linnaeus, illustrating changes in enamel pattern which would result from various stages of attrition. Natural size. (Original.)

3. "The antero-posterior diameter of the last molar (m^3), however, is relatively small at first, and increases continually as the tooth is worn away."

4. "The antero-posterior diameter of the grinding surfaces of all

the intermediate teeth are greater at the stage when the tooth has just fully come into use; . . . from this point the antero-posterior diameter diminishes very rapidly for a short distance and then continues to diminish more gradually to the roots of the tooth."

5. After the tooth has just come fully into use "the transverse diameters of p^3 to m^2 inclusive remain about the same, diminishing slightly near the roots; p^2 gradually diminishes while m^3 increases in transverse diameter as the crown wears away."

6. "The antero-posterior diameter of the protocone in all the teeth of the series remains the same for the whole length of the crown."

7. "Owing to the very slight variation of the transverse diameters of the crowns of p^3 to m^2 inclusive . . . and to the great shortening of their antero-posterior diameters, the ratio of these diameters is very different in old and in young individuals of the same species. Thus in the little worn condition . . . the antero-posterior diameter is always greater than the transverse. As the crown wears away . . . a stage is reached where the two diameters are about equal, then, as the antero-posterior becomes still more shortened, the transverse exceeds it. In every series this variation in ratio seems always to be more advanced in m^1 and m^2."

The present writer has not observed any conflict with these views. The transverse diameter (or "breadth") of the crown and the antero-posterior diameter ("length") of the protocone do, however, decrease to a very slight degree with wear, though their ratio remains constant. Gidley made no comments on the precise effects of wear on the complexity of the enamel folds, and the present writer has therefore attempted by means of serial sections of a number of teeth to ascertain which folds are most affected by wear and which least. As a result, the following generalisations, though based on comparatively little material, appear to be possible.

II. *Changes in Enamel Complexity.*

(a) *In the Upper Teeth.*

1. The pli-protoloph may disappear completely when the tooth is as little as half worn, and is always the most affected of the fossette folds.

2. The pli-hypostyle and pli-prefossette suffer rapid reduction in size but have not been observed actually to disappear.

3. The secondary small plications in the regions of the pre- and postfossette folds proper disappear rapidly if they are of an angular or saw-tooth nature, but may survive a considerable degree of wear if they have the form of rounded loops.

4. The pli-protoconule and pli-postfossette are the least affected of the fossette folds.

5. The hypoglyph becomes shallower with wear but does not normally disappear.

6. The pli-caballin does not disappear with wear in the premolars unless initially very small, but may do so in the molars.

7. The halves of the ectoloph become slightly flattened with advanced wear.

(b) *In the Lower Teeth.*

1. The folding of the entoflexid lobe may be very complex in the earliest stages of wear, but becomes rapidly simplified and does not normally survive the half-worn condition of the tooth.

C. Variability within the Species.

I. *Transverse Diameter of the Crown.*

As Gidley has shown, the transverse diameters over the enamel of the teeth (excluding the second premolar and third molar) are subject only to relatively slight variation within a species. In a series of ten skulls of *Equus caballus** ranging from a large draught horse to a small Texas pony, he notes a difference in the transverse diameter of the second molar of only 2·5 mm. or about 10 per cent. In the third premolar of the same individuals, however, his figures show a difference of 4·5 mm. or nearly 20 per cent., and this range of variation agrees with the present writer's findings in the case of the zebrine group. In the many skulls of *Equus burchellii**, *Equus zebra** and *Equus quagga** which have been examined, the extreme variations in transverse diameter amount to about 20 per cent. of the mean value, but at least 70 per cent. of the specimens in each species are very close indeed to this mean value. The transverse diameter of the cheek teeth is thus subject to a variation of about plus or minus 10 per cent. from a predominant mean value, and this value is therefore a useful characteristic of a species (except in the anterior and posterior teeth). The same relative figures apply to the lower teeth.

II. *Length and Form of the Protocone.*

(*a*) The form of the protocone, and particularly the *relative* anterior and posterior development or elongation, is a very constant character in a species.

(*b*) The absolute length of the protocone is subject within a species to a variation of as much as 30 per cent. between corresponding teeth. In general, the ratio of the length of the protocone to the transverse diameter of the crown is not affected by wear, and this ratio (which we may term the "protocone ratio") is not quite as variable as the absolute length of the protocone. In *Equus caballus** the average value of the protocone ratio

$$\frac{\text{length of protocone}}{\text{transverse diameter of crown}}$$

is 0·48 in the fourth premolar; in the corresponding tooth of *Equus asinus** 0·41; *Equus burchellii** 0·41; *Equus zebra** 0·40; *Equus quagga** 0·44. Though subject to a variation of plus or minus 15 per cent., and thus having no precise significance since values would overlap considerably, the protocone index might be a useful indication of the relative development of the protocone in a species. It must be remembered, however, that in addition to variation between corresponding teeth, the value of the protocone ratio will change from the second premolar to the third molar. In *Equus caballus** average figures are p^2 0·38, p^3 0·45, p^4 0·48, m^1 0·47, m^2 0·52, m^3 0·62.

III. *The Enamel Folds.*

A wide variation is found in the degree of complexity of the enamel folding within a species, but the following generalisations appear from the writer's investigations to be applicable to the upper teeth.

1. The caballine fold is not infrequently absent in particular teeth of an individual of a species which normally shows a strong caballine fold. Even though in some species it is apparently never present, it has no precise value.

2. The pli-protoloph is of very variable development and unless very strong is of no specific value.

3. The degree of development of the pli-hypostyle and pli-prefossette, and the secondary plications of the latter, is variable and of slight value only.

4. The pli-protoconule and pli-postfossette appear to be of very constant development and their presence or absence can be considered as of diagnostic importance.

5. In some species the hypocone shows a consistent slight bulge into the medivallum, giving it the appearance of a partial isolation from the metaconule, and this character seems to be of some determinative value.

6. The flattening of the inner wall of the protoconule appears to be a character of minor diagnostic value in some species.

7. The depth of the hypoglyph is a moderately constant feature.

IV. *The Ectoloph and Styles.*

1. Except in the second premolar and third molar, the nature of the halves of the ectoloph, more particularly the anterior one, is of fairly constant character, being either concave inwards as seen in *Equus caballus** and *Equus burchellii**, or else flattened or even convex as in *Equus asinus**, *Equus zebra** and *Equus quagga**.

2. The three styles, parastyle, mesostyle and metastyle, show quite a considerable range of variation in detail within a species in addition to the difference shown between premolars and molars. The characters of the metastyle are of no specific value, and neither the absolute size nor the grooving of the parastyle and mesostyle are entirely constant characters though they may be useful ones. The degree of isolation of the mesostyle and parastyle from the walls of the ectoloph or their easy confluence with them, however, appears to be a valuable specific character. Owing to the normal relative reduction in size of the styles in the true molars, their isolation is less apparent in these teeth than in the premolars.

V. *The Lower Teeth.*

To quote from Gidley, "the characters of the lower teeth are, in general, affected in the same way as the upper, and seem to be of even less value in determining the species". With these conclusions the present writer is in agreement, in that the very simplicity of structure of the lower teeth deprived them of many of the characters which might be of value in making distinctions. The range of normal variation within a species thus permits of considerable overlap between what are actually different species (as is only too clearly seen in the zebrine group of horses), and thus absolute size must be the chief determinative factor. Other useful, though not entirely constant characters, are (*a*) the shape of the outer walls of protoconid and hypoconid, (*b*) the shape and degree of separation of metastylid and metaconid, (*c*) the size and form of the metaflexid and entoflexid lobes, (*d*) the relative size of the stylids and conids, (*e*) the development of the ectostylid fold* in the hypoconid.

* Called "pli-caballinid" by Stirton (1941).

General Conclusions.

As a result of the examinations made, second premolars and third molars cannot be regarded as providing adequate material for determination, and no species founded on a second premolar or a third molar can be regarded as valid. If second premolars and third molars are known in a species from certain association with determinable teeth, corresponding teeth showing close agreement can then be assigned to the species with fair certainty. On general grounds of size and complexity, isolated second premolars and third molars may be referred to a species as "cf. species".

In the remarks which follow, only the third and fourth premolars and the first and second molars are regarded as exhibiting characters of value in specific determination.

The position of the tooth in the series affects two main characters as follows:—

1. The transverse diameter of the crown, measured over the enamel, is about 5 per cent. greater in premolar than in molar teeth.

2. The enamel pattern is somewhat more complex in the premolar than in the molar teeth, the fourth premolar showing the most complex and the first molar the simplest enamel folding. The mesostyle is somewhat reduced in size in the upper molars, and the entoflexid lobe is smaller in the lower molars than in the premolars.

Bearing in mind the position of the tooth in the series, and the effect upon it of the above factors, the following generalisations may be made with regard to the definition and identification of equine species:—

1. The transverse diameter ("breadth") measured across the enamel is a character of considerable value in determination. The normal departure in size is not more than 10 per cent. and the maximum variation 20 per cent. *If the transverse diameter of a tooth departs by more than* 20 *per cent. from the measurement of the type, it cannot be regarded as belonging to the same species.* If several teeth of a species are known, the possible range which would exclude a specimen will be further reduced and a departure of 15 per cent. may be regarded with suspicion. It must be remembered, however, that different species overlap in point of size, and that *size alone* is not a sufficient basis for determination.

A. *In Upper Cheek Teeth.*

The following factors may be regarded as of reasonable constancy and value in determination:—

1. The relative anterior and posterior development and form of the protocone. (The *absolute* size of the protocone is subject to a variation between premolars and molars of as much as 20 per cent.)
2. The form of the ectoloph and styles.
3. The presence or absence of the pli-protoconule and pli-postfossette and their degree of development.

The following factors may be regarded as of confirmatory value:—

(*a*) The partial isolation of the hypocone (or the lack of such isolation).
(*b*) The protocone ratio (subject to a variation of 30 per cent.).
(*c*) The *presence* of any or all of the following folds, though their *absence* cannot be regarded as significant:—

(i) Pli-hypostyle.
(ii) Pli-caballin (particularly in true molars).
(iii) Pli-protoloph (least reliable).

(*d*) The form of the inner wall of the protoconule.
(*e*) The depth of the hypoglyph.

B. *In Lower Cheek Teeth.*

The following factors may be regarded as of reasonable constancy and value in determination:—

1. The shape of the outer walls of the protoconid and hypoconid.
2. The relative development, degree and mode of separation of the metastylid and metaconid.

The other factors which, though variable, may be regarded as of confirmatory value are:

(*a*) The size and shape of the entaconid.
(*b*) The relative sizes of the stylids and conids (if unusual).
(*c*) The development of the ectostylid ridge or fold in the anterior wall of the hypoconid.
(*d*) The size and form of the metaflexid and entoflexid lobes.

Family EQUIDAE.

Genus Eurygnathohippus van Hoepen 1930.

Genotype: *Eurygnathohippus cornelianus* van Hoepen.

Broad mandibular symphysis with the four first and second incisor teeth large, anteriorly flattened and arranged almost in a straight line, each incisor showing the cup or "Mark"; the third incisors small and lying behind and in contact with the second incisor. (The cheek teeth are unknown.)

Eurygnathohippus cornelianus van Hoepen.

Eurygnathohippus cornelianus van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 2, pp. 23–24, figs. 20–22.

Type: Anterior portion of lower jaw with incisor teeth. Nas. Mus., No. C.679. (Fig. 8.)

Locality: Uitsoek, near Cornelia, Orange Free State.

Horizon: The "Cornelia" Beds of van Hoepen (1930A).

The following is a translation of van Hoepen's description:—

"There is preserved the anterior portion of the lower jaw. The four incisors are long and broad. The teeth lie deep in the antero-central part of the jaw and their grinding surface is practically horizontal. The teeth are anteriorly flattened. The first incisor has an indistinct groove along the centre of its anterior or lower surface. The second incisor has two such grooves. On the inner surface each tooth has two surfaces, ribbed parallel to the height, which meet in a blunt corner and a thick ridge. The canine is approximately one-third the width of the other teeth; unfortunately both are broken off. The four big incisors each show a large cup or mark, entirely surrounded by enamel and also completely filled by cement. The enamel on the front of the tooth is thick, but on the back it is thin. The two small canines show no mark; they are broken off very low down."

The present writer conjectured on the possibility of the teeth, which van Hoepen regarded as canines, being in point of fact reduced third incisors, and this suggestion was independently put forward by Dr. L. H. Wells to the writer. The writer and Dr. Wells have had the opportunity, through the courtesy of Dr. van Hoepen, of examining the type specimen, and are of the opinion that this is probably the case and that the specimen is that of a female individual, consequently lacking canine teeth. This reduction of the third incisors is not quite such a startling supposition as would be their complete absence,

though, as Dr. van Hoepen has said, it is but a step in that direction. The jaw thus clearly belongs to a horse, presumably a very large one,

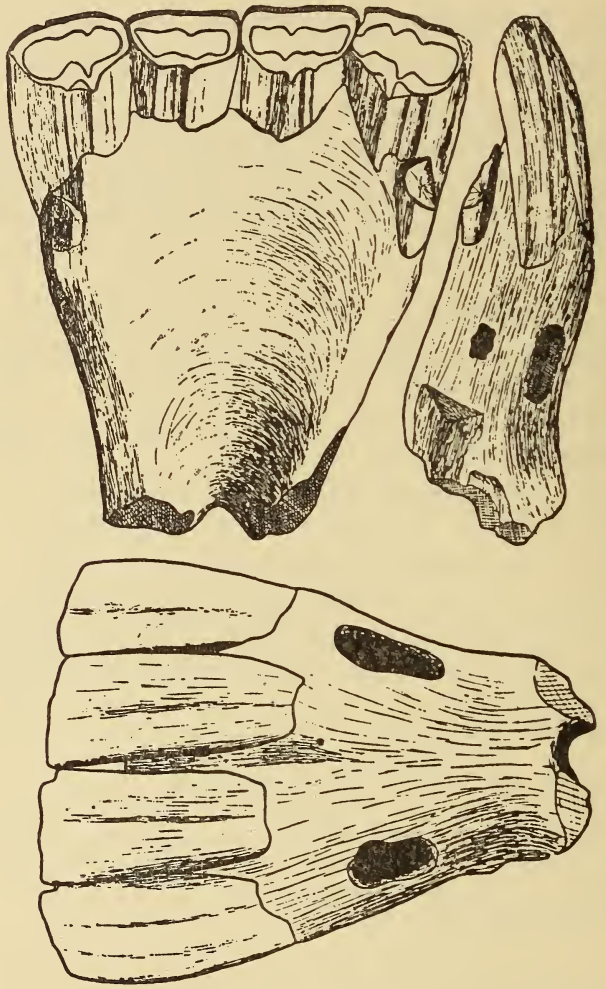


Fig. 8.—Upper, right lateral and lower views of anterior portion of mandible of type of *Eurygnathohippus cornelianus* van Hoepen. Two-thirds natural size. (From van Hoepen.)

but there is some difficulty in absorbing it into *Equus*. Van Hoepen's genus must stand in the mean time, and if "third incisor" be substituted for "canine", his description cannot be bettered.

Genus Notohipparion Haughton 1932.

Genotype: *Notohipparion namaquense* Haughton.

Rather low-crowned heavily cemented hypsodont lower cheek teeth with an extra antero-external cingulum fold or column, either isolated or fused with the parastylid,* present in all the permanent cheek teeth except the second premolar, and a deep groove separating the strongly developed metaconid and metastylid. The upper dentition is unknown.

Notohipparion namaquense Haughton.

Notohipparion namaquense Haughton 1932. Ann. S. Afr. Mus., xxviii, pp. 421–423, fig. 5.

Cotypes: Series lower Pm_2, Pm_3, Pm_4, M_1 and M_3 of the left side and lower M_2 of the right side. S.A. Mus., No. 9982. (Fig. 9.)

Locality: "40 miles east of Springbok in Namaqualand . . ."

Horizon: "from a granite gravel 60 feet down in the surface limestone".

Measurements:

	LPm_2	LPm_3	LPm_4	LM_1	RM_2	LM_3
Breadth . .	16 mm.	17 mm.	17 mm.	16 mm.	14·5 mm.	12·5 mm.
Length . .	29·5 mm.	27 mm.	26 mm.	23 mm.	24 mm.	29 mm.
Height . .	14·5 mm.	17·5 mm.	25 mm.	23 mm.	30 mm.	34 mm.

The following is Haughton's description of the material:—

"The lower teeth upon which this new genus is founded, indicate a stage of equine evolution not hitherto discovered in South Africa. They consist of a series from pm^2 to m^1, together with m^3 of the left side, and pm^4, m^1 and m^2 and a part of m^3 of the right side, obviously of the same individual. As preserved the teeth are all low, the height not being much greater than the length. The main features can be distinguished from the drawings given. In all the teeth the metastylid column is separated from the metaconid column to the base of the crown, and the former projects further inwards than the metaconid or the entaconid, whilst its posterior flange overlaps the anterior border of the entaconid. The antero-external cingulum fold [protoconid fold] is prominent to the grinding surface, being fused with the parastylid in pm^3 and m^1, but still separated from it in pm^4, m^2 and m^3. In pm^4 of the right side (but not of the left), in m^1 and m^2, there

* As defined by Osborn. Stirton (1941) replaces this by "paralophid" and uses "parastylid" for the antero-external column. Such reapplication of an existing name is too confusing to be accepted. Dr. L. H. Wells has suggested to the writer that this extra fold might be termed the "protoconid fold".

is an ectostylid pillar, which near to the root fuses with the wall of the hypolophid to form an ectostylid ridge. Enamel fairly wavy. Teeth heavily cemented" (pp. 421, 422).

"Unfortunately nothing is known of the sequence of gravels and limestone encountered in the well from which *Notohipparion namaquense* was obtained, and but little light can be thrown upon its age. The valleys of Namaqualand seem to have suffered a progressive infilling with sand from Upper Cretaceous times onward; but the process was, in all probability, not a continuous one and further study will probably reveal breaks in the sedimentation. In so far as comparison is possible, *Notohipparion* would seem to represent an early Pliocene stage of equine evolution" (p. 425).

In view of the fact that teeth of another member of the *Hipparion* group occur in the Vaal River gravels associated with well-made stone implements, it would appear that these forms have survived in this region until a much later time than elsewhere. Though *Notohipparion* is quite possibly a Pliocene form, it need not necessarily be "early Pliocene" as Haughton suggests, and it is included here since its horizon is so uncertain and since it may have a bearing on the undoubted Pleistocene forms.

Genus Stylohipparion van Hoepen 1932.

Genotype: *Stylohipparion steytleri* (van Hoepen).

(=*S. hipkini* van Hoepen).

High-crowned rather narrow hypsodont lower cheek teeth with a strongly developed isolated pillar external to the ectosylid, possessing no external groove between hypoconid and hypoconulid, having narrow protoconid and hypoconid and small rather widely separated metaconid and metastylid.

High-crowned upper cheek teeth with isolated oval protocone and possessing a small flange on the antero-internal side of the parastyle.

Stylohipparion steytleri (van Hoepen).

Hipparion steytleri van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 2, pp. 21–23, figs. 14–19.

Stylohipparion hipkini van Hoepen 1932. Pal. Nav. Nas. Mus. Bloemfontein, II, 3, pp. 31–32, figs. 14–17 and 18–20.

Stylohipparion steytleri van Hoepen 1932. *Ibid.*, pp. 33–35, figs. 21–23.

Fig. 9.—Series of lower cheek teeth of the type of *Notohipparion namaquense* Haughton. Natural size. (From Haughton.)

Type: Upper M^1 or M^2 of the right side. Nas. Mus., No. C.558. (Fig. 10.)

Locality: Uitsoek, near Cornelia, O.F.S.

Horizon: The "Cornelia Deposits" of van Hoepen.

Measurements:

Breadth . . .	22 mm.
Length . . .	22 mm.
Height . . .	54 mm.

Paratypes: Upper M^3 of the left side. Nas. Mus., No. C.555. (Fig. 10.)

Lower M_1 and M_2 of the left side. Nas. Mus., No. C.556. (Fig. 10.)

Measurements:

	LM^3	LM_1	LM_2
Breadth . .	18 mm.	10(12) mm.	10·5(12·5) mm.
Length . .	21 mm.	broken	21 mm.
Height . .	66 mm.	32 mm.	41 mm.

(The figures in brackets include the accessory outer column.)

Upper Teeth.

The halves of the ectoloph are concave inwards though the posterior half may be flattened. The metastyle is small and the mesostyle and parastyle narrow, the latter having an unusual anterior flange or groove. The protocone is isolated and oval in shape with a somewhat flattened interior face. A small tongue projects into the medivallum towards the protocone. The hypocone is very small, being less than one-third the size of the protocone. A deep, sometimes double protoconule fold is present and, with the prefossette folds, tends to isolate the postero-internal corner of the prefossette. Protoloph, hypostyle and postfossette folds are present and are of moderate depth. Secondary plications are present in the region of the prefossette fold and appear to be persistent.

Lower Teeth.

Protoconid and hypoconid are rather narrow transversely and have slightly flattened or even concave outer walls. An ectostylid ridge or fold is present in the anterior wall of the hypoconid, and external to this is a stout oval pillar arising from the cingulum and reaching

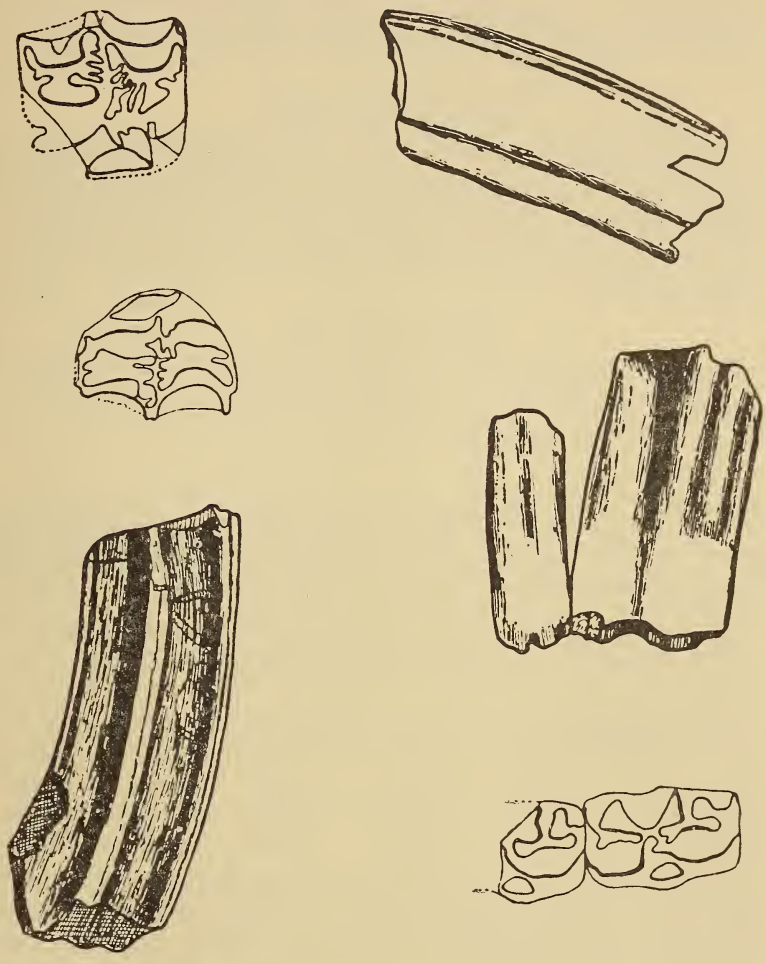


Fig. 10.—*Stylohipparion steytleri* (van Hoepen).
Top: Type upper right second (or third) molar; crown and anterior views.
Left: Paratype upper left third molar; crown and outer lateral views.
Right: Paratype lower left first and second molars; inner and crown views.
All natural size. (From van Hoepen.)

almost to the unworn crown. There is no external groove marking off hypoconid and hypoconulid. The entaconid is small, and the metaconid and metastylid are rather small and widely separated by a rounded groove. The entoflexid lobe is only slightly longer than the

metaflexid lobe, and folding in their walls is slight or lacking, a small notch in the anterior of the entoflexid lobe being sometimes present.

Referred Upper Teeth.

An upper second (or possibly third) molar of the left side has been recovered from the Vaal River deposits at Christiana, probably from Younger Gravels. This specimen (Arch. Sur., No. 113) is considerably worn, but retains all the characters shown by the less worn type and paratype.

Referred Lower Teeth.

Five lower teeth, being a series from LPm_3 to LM_3 from the type locality, were referred to this species by van Hoepen (1932), and the enamel pattern of four of them is shown in fig. 11.

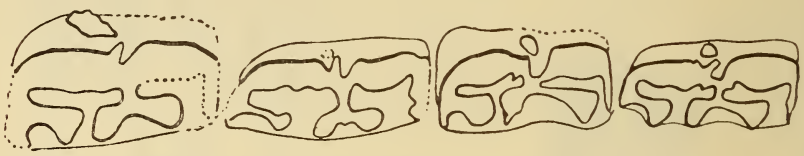


Fig. 11.—Referred series of lower left cheek teeth of *Stylohipparion steytleri* (van Hoepen). Crown views. Natural size. (From van Hoepen.)

The following are the dimensions of these teeth (as preserved):—

	LPm_3	LPm_4	LM_1	LM_2	LM_3
Breadth . .	15 mm.	12 (14) mm.	12 mm.	11·5 mm.	9 mm.
Length . .	25 mm.	28 mm.	22 mm.	24·5 mm.	23 mm.
Height . .	64 mm.	74 mm.	69 mm.	73 mm.	38 mm.

A lower second molar from the type locality was described by van Hoepen in the same paper (1932) as the type of a new species, *S. hipkini*. The specimen (Nas. Mus., No. C.797) is very little worn and thus exhibits an entirely uncharacteristic pattern. Its height is 81 mm., and 15 mm. below the exposed grinding surface the dimensions of the tooth are: breadth 12·5 mm., length 26·5 mm.; in the middle of the tooth the corresponding dimensions are 13 mm. and 22 mm. A left second premolar is provisionally referred to this new species, but there does not appear to exist any valid reason for separating either of these teeth from the earlier species.

Two lower teeth recovered by Broom from the Kromdraai Cave have been referred by the present writer to this species but they have not yet been described.

Genus Equus Linnaeus 1758.

Genotype: *Equus caballus** Linnaeus.

*Equus burchellii** (Gray).

*Asinus burchellii** Gray 1824. Zool. Journ., 1, p. 247, pl. 9, figs. 1, 2.
*Equus quagga wahlbergi** of most authors.
Equus platyconus van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 1, pp. 4–5, figs. 3–5.
Equus simplicissimus van Hoepen 1930. *Ibid.*, p. 6, fig. 7.
Equus simplicissimus van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 2, p. 21, figs. 12, 13.
Kraterohippus elongatus van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 1, pp. 7–8, fig. 9.
Equus lylei Dreyer 1931. "New Fossil Mammals and Man", p. 30, pl. v, fig. 9; pl. vi, figs. 6, 7, 8; pl. vii, fig. 8.

The general dental formula is the same as in *Equus caballus**, but the vestigial first upper premolar, which is normally lacking in *E. caballus** and in most other members of the genus, is frequently present in *E. burchellii** and is shed only comparatively late in life. The upper incisor teeth closely resemble those of *E. caballus**, but the lower incisors all typically lack the cup or mark so characteristic of the common horse. This cup is normally formed as a result of closure of two posterior folds of the tooth, and its incomplete formation is well seen in many specimens of *E. asinus**. In *E. burchellii** it is completely absent in the lower I_3, partially formed in I_2 and partially or completely formed in I_1, but even if present in I_1 is so shallow as rapidly to disappear with wear. A typical specimen is shown in fig. 12. This feature is not characteristic of either *E. zebra** or *E. quagga**, though in the latter species the cup is often absent in the lower third incisor, and is not as deep as in *E. caballus**. The retention of the vestigial first premolar and the nature of the incisor teeth may both be regarded as rather primitive characteristics.

The upper cheek teeth are a good deal smaller than those of *E. caballus**, and the dimensions of a typical complete dentition (Tvl. Mus., No. 173, fig. 13*c*) in normal wear are:

	Pm^2	Pm^3	Pm^4	M^1	M^2	M^3
Breadth .	22 mm.	24 mm.	24·5 mm.	23 mm.	23 mm.	21 mm.
Length .	35 mm.	24 mm.	23·5 mm.	20·5 mm.	21 mm.	23 mm.

The breadth variation noted in Pm^3–Pm^4 is 22-26 mm. and in M^2–M^1 is 21–25 mm.

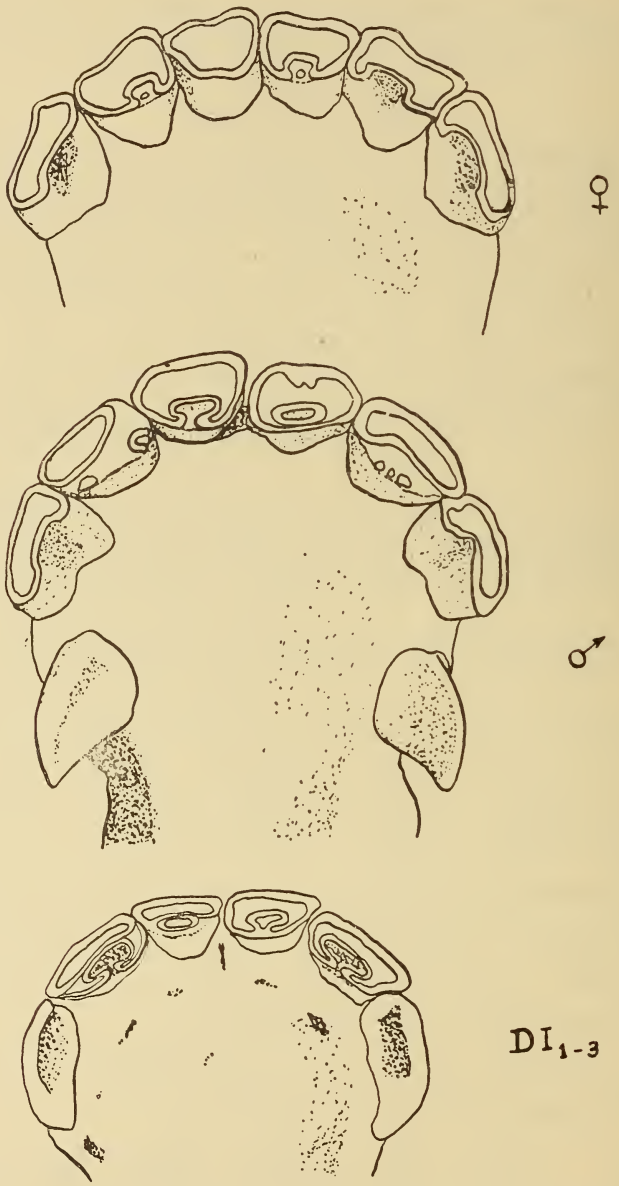


Fig. 12.—Lower incisor teeth of *Equus burchellii** (Gray) to show the characteristic absence or reduction of the cup or "mark". Natural size. (Original.)

The halves of the ectoloph are concave from without inwards and curve smoothly into the styles, though the mesostyle may overhang slightly. The parastyle is commonly obliquely flattened anteriorly in the premolars but less commonly so in the true molars. This and the mesostyle are sometimes grooved externally for a small extent below the grinding surface. The metastyle is small and not prominent. The protocone is elongate oval in form (proportionally narrower than in *E. caballus**), and the portion anterior to the junction with the protoconule comprises about one-third of the total protocone length (except in Pm^2 where the anterior extent is very small in all species of *Equus*). The hypocone is not large and frequently shows a slight bulge into the medivallum, giving to it the appearance of a tendency towards isolation from the metaconule. The caballine fold is typically absent, but may be present in some individuals, particularly in the premolars. The fossette folds are generally small except for a well-developed pli-protoconule and a fairly good pli-postfossette. The pli-hypostyle and pli-prefossette are very variable in development, but the pli-protoloph is usually present and often fairly deep. The crown patterns of three typical dentitions are shown in fig. 13.

The lower teeth are also a good deal smaller than those of *E. caballus**. The dimensions of the lower teeth (fig. 14) in the individual for which the measurements of the upper teeth have already been given are:

	Pm_2	Pm_3	Pm_4	M_1	M_2	M_3
Breadth . .	12·5 mm.	13·5 mm.	14 mm.	12 mm.	11·5 mm.	11 mm.
Length . .	28 mm.	25 mm.	24 mm.	22 mm.	23 mm.	27 mm.

The breadth variation noted in Pm_3–Pm_4 is 12–15 mm. and in M_2–M_1 is 11–14 mm.

The outer walls of the protoconid and hypoconid are both flattened or even concave inwards, and the ectostylid fold in the hypoconid is small or even absent. The entaconid is small and somewhat quadrate in form. The metaconid is oval, and is separated from the metastylid by a fairly sharp-pointed groove. The metastylid itself is rather small, pear-shaped and bluntly pointed. The metaflexid lobe is smaller than that of the entoflexid, and the outer walls of the entoflexid may show some folding which does not persist with advanced wear.

Referred Fossil Material.

Petrified specimens of this species are of common occurrence in cave deposits, in superficial deposits, in river gravels and elsewhere. Such

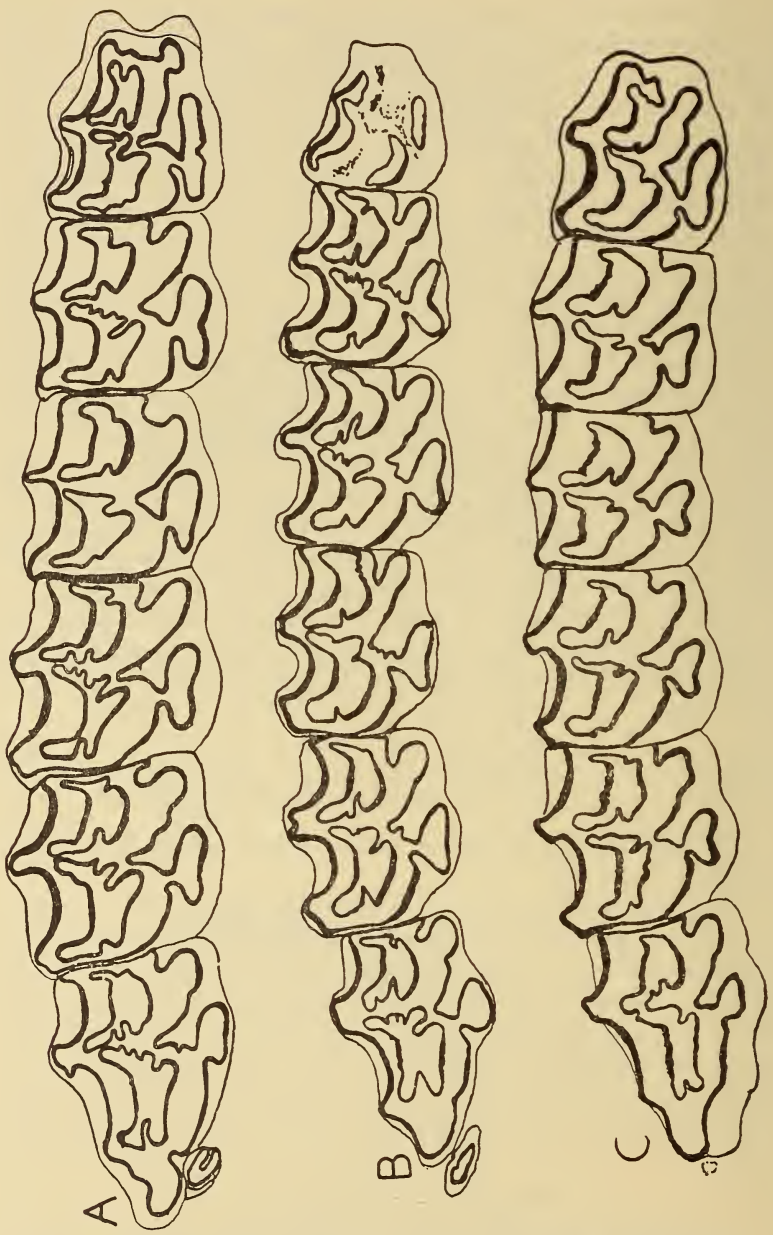


Fig. 13.—Left upper cheek teeth of *Equus burchellii** (Gray). The upper dentition C belongs to the individual figured in fig. 14, C. Natural size. (A, after Owen; B and C original.)

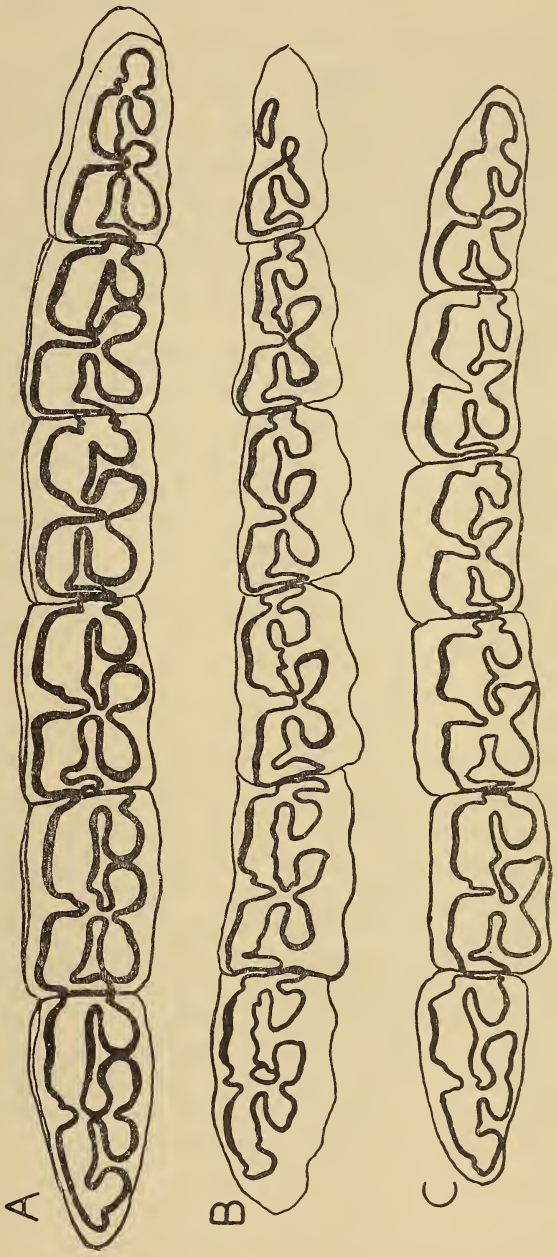


Fig. 14.—Right lower cheek teeth of *Equus burchellii** (Gray). The lower dentition C belongs to the individual figured in fig. 13, C. Natural size. (A, after Owen; B and C original.)

material does not always seem to be of very great antiquity and is quite possibly only of Upper Pleistocene Age.

The species *Equus platyconus* van Hoepen and *Kraterohippus elongatus* van Hoepen have already been regarded by Haughton (1932) in his revision as probable synonyms of the living Burchell's zebra, and there seems no reason to doubt the correctness of this conclusion. *Kraterohippus elongatus*, moreover, is founded on a broken upper Pm^2, almost certainly incorrectly restored and is valueless as a type. *Equus simplicissimus* van Hoepen also appears to fall well within the range of variation of the living species and does not warrant distinction.

Equus lylei Dreyer, founded on well-mineralised material from the springs at Floris Bad, was regarded by Haughton as falling within the range of variation of the living species. This is certainly the case, most of the specimens from the type and neighbouring areas, however, lying close to the lower size limit of the species. Their enamel characters are quite typical and the material does not apparently require specific distinction, though a varietal or sub-specific separation may prove to be justified.

Mineralised specimens of *Equus burchellii** occur in the deposits of the Vaal River basin.

*Equus zebra** Linnaeus.

*Equus zebra** Linnaeus 1758. Syst. Nat., Ed. 19, 1,

The incisor teeth have been considered under *E. burchellii** above.

The upper cheek teeth differ very little in size from those of *E. burchellii**, though on the average they are possibly a millimetre broader than the average bontequagga. The halves of the ectoloph are almost straight or even slightly convex, and the parastyle and mesostyle are somewhat abruptly marked off from the ectoloph walls. These features are less apparent in the true molars than in the premolars. The protocone is sub-triangular rather than oval, and the portion anterior to its junction with the protoconule is less than one-third of the protocone length. The parastyle is commonly flattened anteriorly but is not as obliquely directed as in *E. burchellii**. The hypocone is only a little smaller than the protocone. A caballine fold is often, but not consistently, present. The fossette folds are all small, and even the pli-protoconule and pli-postfossette may be virtually lacking. The pli-protoloph is typically absent or extremely small.

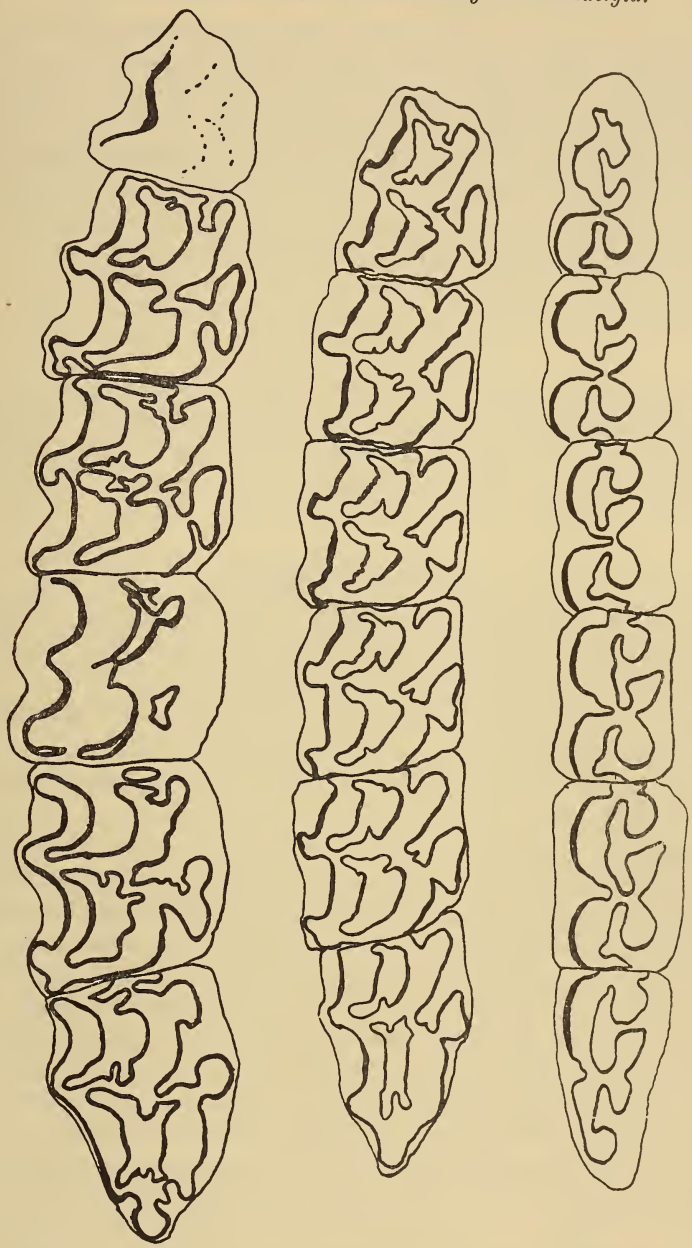


FIG. 15.—Two left upper and a right lower series of cheek teeth of *Equus zebra** Linnaeus. Natural size. (Original.)

The lower teeth are also comparable in size with those of the bontequagga. The outer walls of the protoconid and hypoconid are convex and well rounded, and the ectostylid fold is small or lacking. The entaconid is rounded, as also is the metaconid, but the metastylid is pear-shaped and rather pointed. The groove separating metaconid and metastylid is somewhat pointed. The metaflexid and entoflexid lobes are simple.

Two upper and a lower dentition are shown in fig. 15.

Referred Fossil Material.

The only petrified specimens certainly to be ascribed to this species were recovered from the Cango Caves near Oudtshoorn, but the remains of zebrine skulls are not uncommon in the older dune sands of the coastal belt in the Cape Province.

*Equus quagga** Gmelin.

*Equus quagga** Gmelin (Linnaeus 1788). Syst. Nat., Ed. 13, 1, p. 21.
*Equus quagga** Cooke 1941. S. Afr. J. Sci., xxxvii, p. 307.
*Equus quagga** Shapiro 1943. S. Afr. J. Sci., xxxix, p. 117.
(non *E. quagga quagga** Dreyer 1931. "New Fossil Mammals and Man", p. 33.)
(non *E. quagga** var. Haughton 1932. Ann. S. Afr. Mus., xxviii, p. 424.)

*Equus quagga** became extinct in 1872 before most museums had commenced the collection of skeletal material from Southern Africa, and only a cast in the Transvaal Museum, taken from a skull in the possession of the Stuttgart Museum, represents a specimen actually known to be that of the true quagga. This individual was very young, and the cast is not of great value for identification purposes. Fortunately the great Richard Owen, in the "Philosophical Transactions of the Royal Society of London" for 1869, gives natural size figures of the dentition of a good adult specimen at that time in the Royal College of Surgeons. Dr. Robert Broom, while in London many years ago, made drawings of the teeth of a quagga in the British Museum collections, and these agree with those given by Owen in all characters. Some old skulls and jaws in the McGregor Museum, Kimberley, and in the collections of the Kingwilliamstown Museum, agree closely with the figures published by Owen and with

the manuscript drawings given to the writer by Dr. Broom, and as these skulls were collected in a region certainly at one time overrun by quagga, this material may with fair certainty be taken to represent the species. Furthermore, the characters which Owen remarks as distinguishing the quagga from the other two South African species, are present in these skulls.

From the limited material available, it would appear that the teeth of this species do not differ very markedly in size from those of the zebra and bontequagga. The largest and smallest upper dentitions in the McGregor Museum collection (fig. 16, B, C) have the following dimensions over the enamel:—

	Pm^2	Pm^3	Pm^4	M^1	M^2	M^3
Breadth .	21·5 mm.	22·5 mm.	22·5 mm.	20·5 mm.	20·0 mm.	19·5 mm.
Length .	30·5 mm.	23·5 mm.	21·5 mm.	20·0 mm.	19·5 mm.	20·5 mm.
Breadth .	23·0 mm.	27·0 mm.	26·5 mm.	24·5 mm.	24·0 mm.	19·5 mm.
Length .	32·5 mm.	24·5 mm.	24·5 mm.	21·5 mm.	21·5 mm.	23·5 mm.

Owen's figure gives measurements only slightly smaller than the dimensions of the larger dentition, so that it would appear that the average quagga dentition was a little larger than the normal bontequagga, and the range in breadth is somewhat greater as well, being 22–27 mm. for Pm^3–Pm^4 and 20–25 mm. for M^1–M^2.

The halves of the ectoloph are almost straight or even slightly convex, and are abruptly marked off from the parastyle and mesostyle by an acute angle, though this character is suppressed in the third molar and not clear in the second premolar. The external face of the parastyle, unlike that in *E. burchellii** and *E. zebra**, is not directed in an oblique angle anteriorly but lies roughly parallel to the axis of the row of cheek teeth. The protocone is elongate oval or somewhat triangular in form, and commonly has an almost median indentation in its inner wall, giving a rather bilobate appearance. The junction of the protocone with the protoconule is only slightly anterior to the middle of the protocone. The hypocone is small and the hypoglyph is rather variable. The caballine fold is normally absent. The fossette folds are all small, even the pli-protoconule and pli-postfossette being commonly reduced to a small notch only. Nevertheless the pli-protoloph and pli-hypostyle are both normally visible, though the pli-prefossette is typically small or absent. The crown patterns of three upper dentitions are shown in fig. 16.

The lower teeth are comparable in size with those of *E. burchellii**, two typical dentitions measuring:

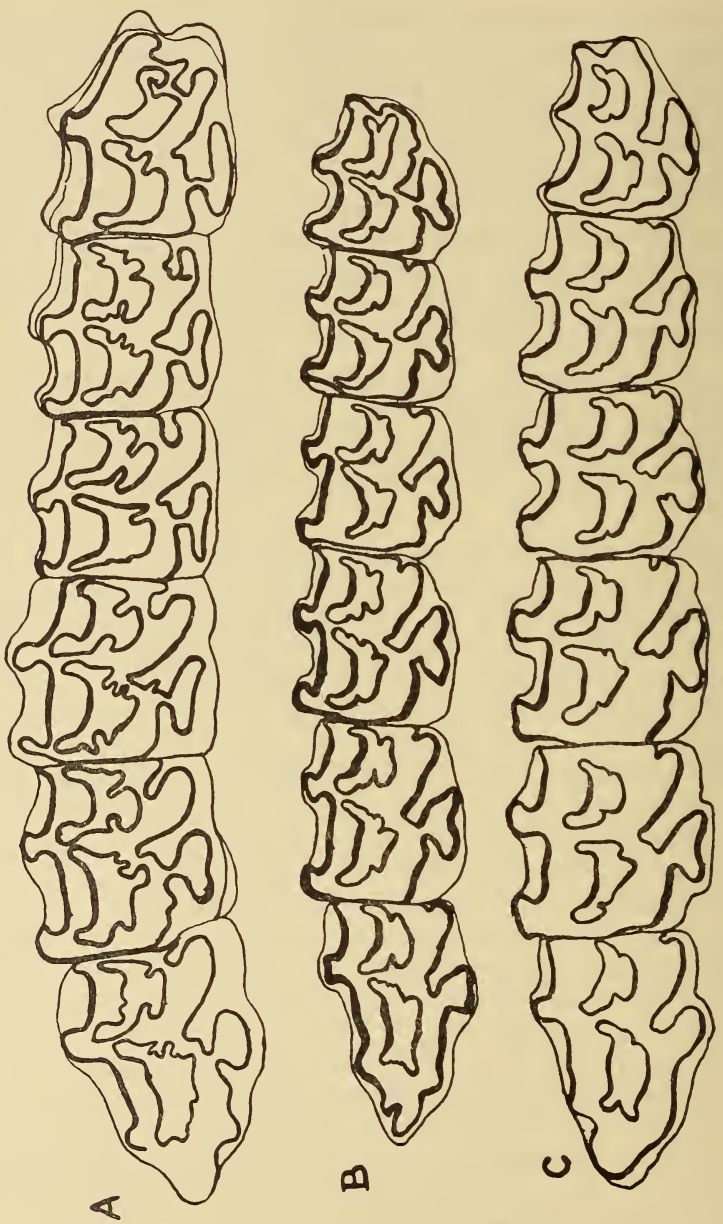


Fig. 16.—Left upper cheek teeth of *Equus quagga** (Gmelin). Natural size. (A, after Owen: B and C original.)

	Pm_2	Pm_3	Pm_4	M_1	M_2	M_3
Breadth .	13·0 mm.	14·0 mm.	14·5 mm.	12·5 mm.	12·0 mm.	11·5 mm.
Length .	27·5 mm.	25·0 mm.	24·0 mm.	22·5 mm.	22·0 mm.	26·0 mm.
Breadth .	13·0 mm.	14·0 mm.	14·0 mm.	12·5 mm.	12·0 mm.	11·0 mm.
Length .	31·5 mm.	26·5 mm.	26·0 mm.	23·5 mm.	24·0 mm.	23·5 mm.

Owen's figure agrees very closely in dimensions with those of the latter species. The probable range in breadth may be estimated as 12–16 mm. for Pm_3–Pm_4 and 11–15 mm. for M_1–M_3.

In character the lower teeth resemble those of bontequagga rather than zebra, for the outer walls of the protoconid and hypoconid are somewhat flattened, the latter more so than the former. The ectostylid fold is often present. The metaconid is rounded or oval, and is separated from a pear-shaped metastylid by a rounded groove. The entaconid is rounded to quadrate and notably larger in the premolars than in the molars.

Three dentitions are shown in fig. 17.

Probably largely in consequence of the confused ideas which have hitherto existed regarding the characters of the teeth of *Equus quagga**, none of the teeth referred to by various authors as "*E. quagga*" or "*E. quagga quagga*" can be regarded as actually belonging to Gmelin's species. These so-called "quagga" teeth are mainly those of *E. burchellii** (Gray) but, remarkably enough, none of the fossil teeth described under other names can be regarded as belonging to *E. quagga** either, so that it would appear that this recently extinct species has not hitherto been recognised to any notable degree in our fossil collections. This species is represented by material in the McGregor Museum, Kimberley, derived from surface deposits at Koffiefontein, Orange Free State. It has also been recorded from a cave near Kuruman (Cooke, 1941), from Bankies, O.F.S. (Shapiro, 1943) and appears to be present in the deposits of the Vaal River valley. Doubtless more material will be recognised in due course.

Equus capensis Broom.

Equus capensis Broom 1909. Ann. S. Afr. Mus., vii, pp. 281–282.
Equus capensis Broom 1913. Bull. Amer. Mus. Nat. Hist., xxxii, p. 437, fig. 1.
Equus capensis Broom 1928. Ann. S. Afr. Mus., xxii, p. 441, fig. 2, A.
Equus cawoodi Broom 1928. *Ibid.*, pp. 443–444, fig. 3, A.
Equus gigas van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 1, pp. 2–3, fig. 1.
Equus capensis Dreyer 1931. *Ibid.*, pp. 36–37, pl. vii, fig. 5.

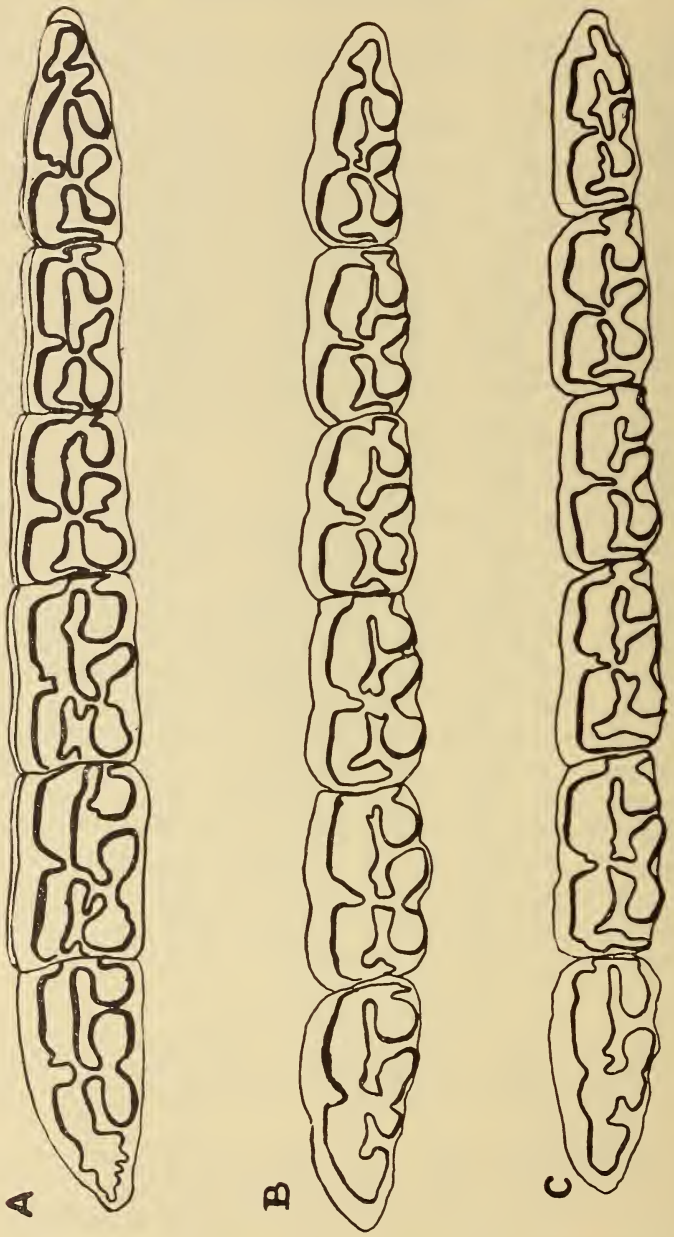


FIG. 17.—Right lower cheek teeth of *Equus quagga** (Gmelin). Natural size. (A, after Owen; B and C original.)

Equus westphali Dreyer 1931. *Ibid.*, pp. 36–37, text-fig.

Equus capensis Haughton 1932. Ann. S. Afr. Mus., xxviii, pp. 410–412, fig. 2.

Equus capensis Cooke 1939. S. Afr. J. Sci., xxxvi, pp. 413–414, fig. 2.

Equus capensis Cooke 1941. S. Afr. J. Sci., xxxvii, pp. 308–311, figs. 4, 5.

Equus capensis Wells and Cooke 1942. Trans. Roy. Soc. S. Afr., xxix, pp. 228–229, fig. 12.

Equus capensis Shapiro 1943. S. Afr. J. Sci., xxxix, pp. 117–178.

(non *E. cawoodi* van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 1, pp. 3–4, fig. 2.)

(non *E. cawoodi* Dreyer 1931. "New Fossil Mammals and Man", pp. 26–29, pl. vi, figs. 8–12; pl. v, fig. 2.)

(non *E. capensis* Broom and Le Riche 1937. S. Afr. J. Sci., xxxiii, pp. 769–770, fig. 1.)

(non pars *E. capensis* Cooke 1939. S. Afr. J. Sci., xxxvi, pp. 413–414, fig. 2*a*.)

Type: Series lower left P_2, P_3, P_4, M_1, M_2 embedded in limestone and damaged on the inner sides. S.A. Mus., No. 658. (Fig. 18.)

Locality and Horizon; Beach debris, Yzerplaats, Maitland, Cape Province.

Measurements:

	LP_2	LP_3	LP_4	LM_1	LM_2
Breadth (damaged)	?	?15+ mm.	15+ mm.	14+ mm.	14+ mm.
Breadth (as restored)	?	19·5 mm.	18·5–19 mm.	18 mm.	17·5 mm.
Length	?30 mm.	?35 mm.	34·5 mm.	31 mm.	30 mm.
Height	?75 mm.	87 mm.	103 mm.	92 mm.	94 mm.

Neotype (Haughton 1932): Lower left fourth premolar. S.A. Mus., No. 2821. (Fig. 18.)

Locality: Saldanha Bay.

Measurements:

	LPm_4
Breadth	18·5 mm.
Length	33·0 mm.
Height	92·0 mm.

The type of this species was first described by Broom in 1909 but was not figured until 1928. It comprises a damaged series of teeth embedded in a slab of sandy limestone found on the beach at Yzerplaats, Maitland district, Cape Province. It would appear that this limestone represents a former land deposit now lying below sea-level

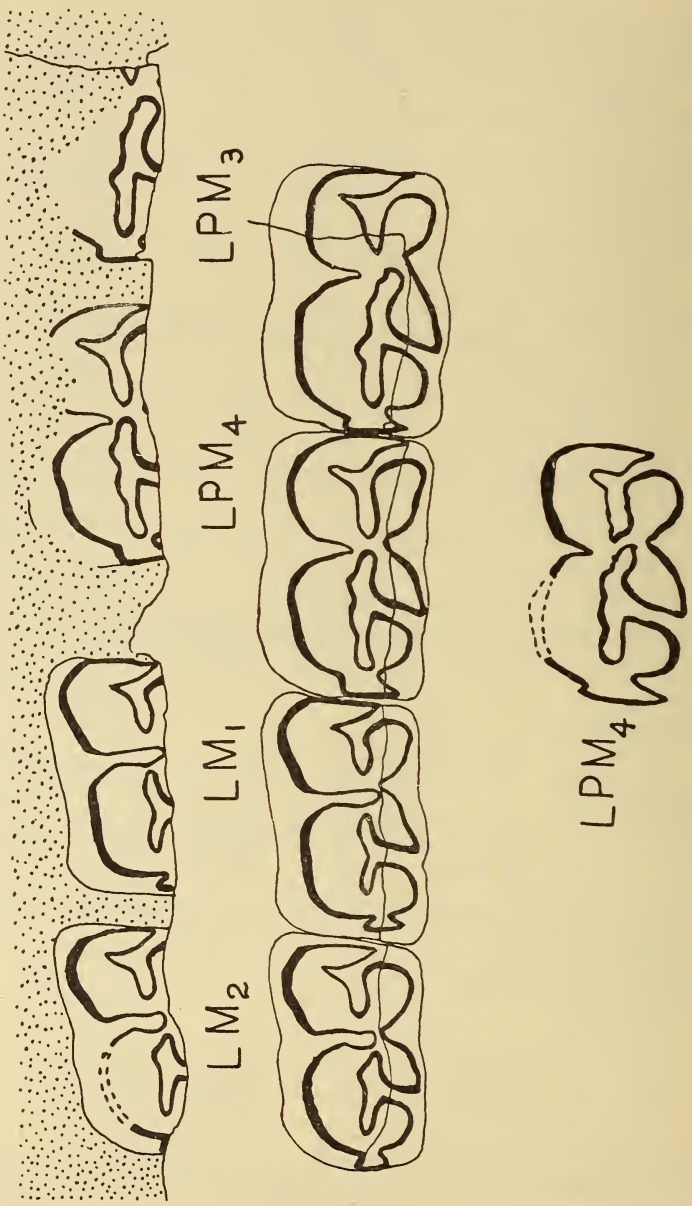


FIG. 18.—*Equus capensis* Broom.

Top: Crown view of the type series of left lower cheek teeth as embedded in the limestone matrix. (Original.)

Centre: Restoration of crown patterns of type series. (Original.)

Below: Enamel pattern of neotype lower left fourth premolar. (From Haughton.)

All natural size.

as a result of late crustal warping. While it is impossible to arrive directly at an estimate of the age of the original deposit, this must antedate the warping which itself is most probably the final crustal warping occurring between the development of the "major emergence" and the "minor emergence" raised beaches. The dating of this event is difficult, but the writer has elsewhere (Cooke, 1941 *b*) suggested that it coincides approximately with the existence of the Stellenbosch industry and may be broadly Middle Pleistocene.

If this estimate is not far wrong, the *Equus capensis* bearing limestone belongs most probably to the Middle Pleistocene, and the general affinities of the teeth also support a Middle Pleistocene age.

The teeth themselves are exposed on a fractured surface of the slab, and the inner portions of each tooth have been lost. The series belongs to the left lower jaw and lacks the third molar, but the second premolar is completely embedded and the anterior portion of the third premolar partly covered by limestone. The patterns of the grinding surfaces are consequently visible only in part of the third premolar, the fourth premolar and the first and second molars, but all the teeth are well exposed in their inner lateral aspects. Broom figured a restoration of these four teeth in 1928, but many features of the drawing are faulty, and the restored portions probably incorrectly given. Fig. 18 shows an accurate drawing of the enamel patterns as they appeared in the slab in 1940, though possibly the specimen is now less perfect than in 1928. Nevertheless, Broom's restoration fails to show the distinct flattening of the hypoconid outer wall, gives incorrectly the shape of the visible portions of the entaconid and simplifies the irregularities in the entoflexid. As Haughton has pointed out: "In his restoration of the missing portions he has shown the metaconid, metastylid and entoconid as being rounded in outline, his restoration of the metastylid in particular differing considerably from the somewhat triangular or pointed form seen in *Equus caballus*." It is impossible from the specimen to see any grounds for maintaining this restoration, and in the light of all the available evidence a new restoration is now given which is probably not far from the truth (fig. 18).

In form these teeth resemble those of the true quagga rather than the other living species, but they are notable for their very large size, far exceeding the dimensions of any living type. The protoconid and hypoconid are well developed, and the outer wall of the latter is more markedly flattened than in the former. The protoconid projects, in the molars at least, beyond the outer wall of the hypoconid, giving a

somewhat lopsided appearance to many of the teeth. The ectostylid fold in the hypoconid wall is small or completely lacking. The hypolophid is quite distinctly marked off from the hypoconid. The entaconid is quadrate to semi-lunate in form with a distinctly angular antero-internal corner ("entostylid"). The metastylid is pear-shaped and somewhat pointed (if the restoration or evidence from the neotype and other specimens can be assumed to be correct). The metaconid is oval and is separated from the metastylid by a pointed groove. The outer wall of the entoflexid is irregular or wavy in the premolars and slightly concave in the molars. The simplicity of the molars as compared with the premolars, and also the rather great disparity of form and size, is striking in some of the series available. The range in breadth for the premolars appears to be about 18·5 to 22 mm. and for the molars 17·5 to 21 mm.

Amongst the large number of lower teeth referred to this species, the best preserved and most valuable series is shown in Fig. 19. These teeth come from a thermal spring at Vlakkraal near Bloemfontein, Orange Free State, and have been described by Wells and Cooke (1942). Their individual dimensions are as follows:—

	Pm_2	Pm_3	Pm_4	M_1	M_2
Breadth	18·5 mm.	19 mm.	19·5 mm.	17 mm.	17·5 mm.
Length	38 mm.	34 mm.	34 mm.	29 mm.	30·5 mm.
Height (excluding roots) .	56 mm.	62 mm.	74 mm.	58 mm.	51 + mm.

The teeth are thus very slightly smaller than those of the type series, but there can be little doubt regarding their close agreement in all essentials. This series also illustrates very well the lateral aspects of the teeth and their normal angles of wear, and is very useful as an aid in determining the position of an individual tooth in a series.

The upper teeth of *Equus capensis* are so far not certainly known, but from the normal relationships between upper and lower teeth the expected breadth of the uppers would be 29 to 35 mm. for the premolars and 27 to 33 mm. for molars. Broom (1913 *b*, 1937), Dreyer (1931) and Haughton (1932) have referred large upper teeth to *E. capensis*. New species within the correct size group have also been erected by Broom (1928), van Hoepen (1930), Dreyer (1931) and Wells (1941). All these finds have been on open sites where association is virtually valueless, but material described by the writer (Cooke 1941 *a*) and by Wells and the writer (1942) from sealed sites may elucidate the problem.

In a large collection of equine remains from the Wonderwerk Cave

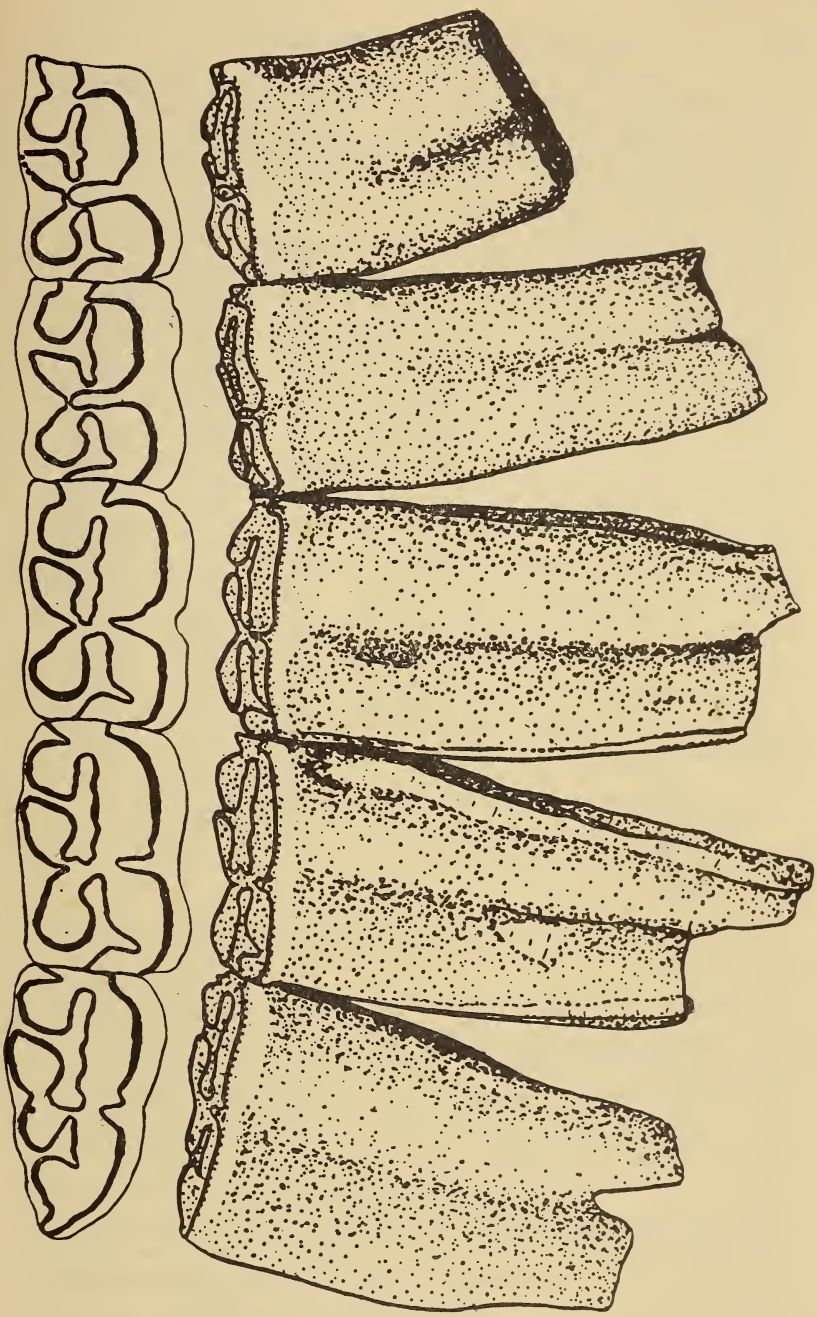


FIG. 19.—Fine series of lower left cheek teeth referred to *Equus capensis* Broom. Outer lateral and crown views. Natural size. (From Wells, Cooke and Malan.)

in the Kuruman district, twelve teeth (upper and lower) were immediately distinguished by their great size. Five are lower teeth which agree in pattern with those of *E. capensis*, though they are very slightly smaller than the type. The associated upper teeth can hardly belong to a different species, and these are closely comparable with the type of *Equus cawoodi* described by Broom (1928) from the Vaal River gravels. The type of *E. cawoodi* (which is most probably a Pm^3 and not a Pm^4 as Broom states) is little worn, and agree in almost every detail with a little worn LPm^4 from Wonderwerk. The Wonderwerk LPm^4 was sectioned, and on its sectional surface showed a very considerably simplified pattern agreeing very well with the uppers referred to *E. capensis* by Broom (1913) and one referred to that species by Haughton (1932). Additional material from Wonderwerk described by Wells (1943) confirms this view. The large upper teeth associated with the fine lower series from Vlakkraal are very worn, but they agree in all essentials with *E. cawoodi* and there can be little doubt that the two species are synonyms. Shapiro (1943) dissented from this view, but his argument was based chiefly upon the material erroneously referred to *E. capensis* by Broom & le Riche and now falls away, as he himself would doubtless agree.

The type RPm^3 of *E. cawoodi* (M.M.K., 3711) has the following dimensions (fig. 20):—

Breadth, on grinding surface (which is very little worn)	31·5 mm.
Breadth, 3 cm. below grinding surface	32 mm.
Length	33 mm.
Height	80 mm.

It may conveniently be taken as a neotype of the upper dentition of *E. capensis*.

The form of the upper dentition of *E. capensis* (as now understood) is very similar to that of *E. burchellii**, of which it is virtually an enlarged version. The halves of the ectoloph are concave inwards and curve easily into the styles, except for a distinct tendency for an anterior overhang of the mesostyle. The parastyle is obliquely flattened anteriorly in the premolars but less noticeably so in the true molars. The metastyle is small. The hypocone is moderately small but the hypoglyph may be rather deep. The caballine fold is sometimes present but may often be absent. The pli-protoconule and pli-postfossette are well marked, but the pli-protoloph and pli-hypostyle are very small and may disappear completely with wear. The pli-prefossette and secondary small postfossette are distinct in

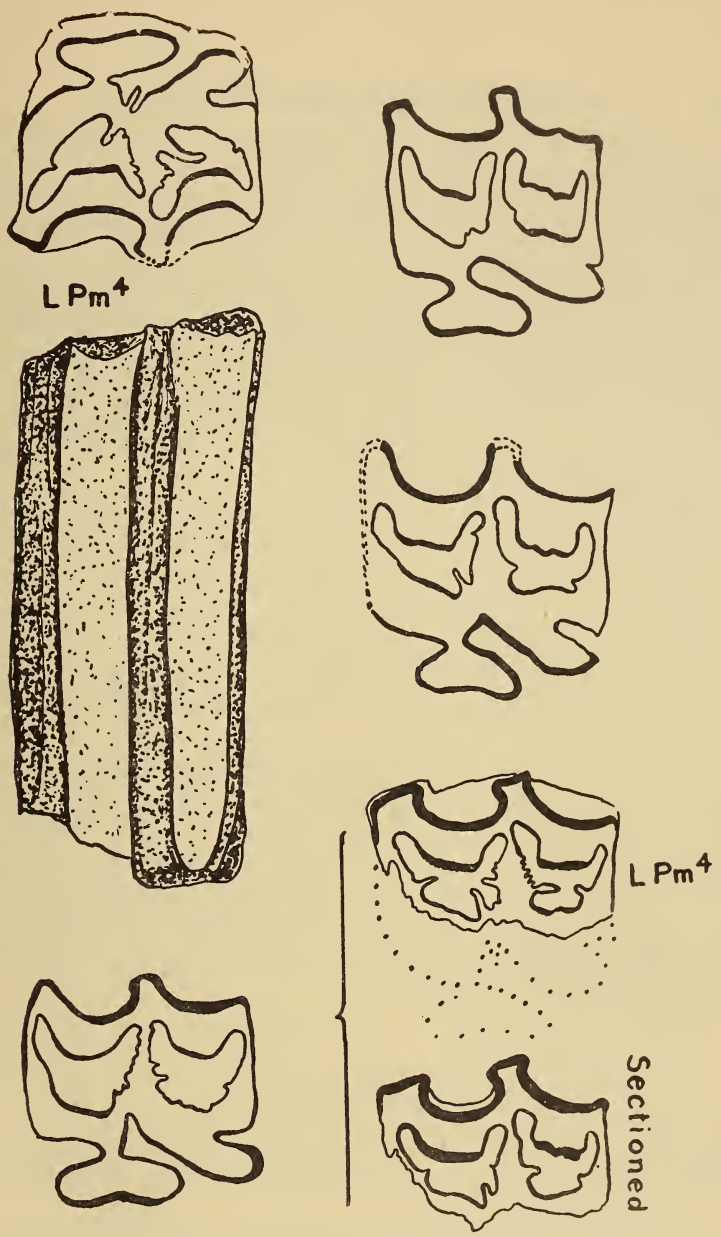


FIG. 20.—*Equus capensis* Broom.

Upper left: Crown and outer lateral views of neotype upper right third premolar. (Original.)

Upper right: Enamel pattern of two referred upper left fourth premolars from Saldanha Bay. (After Broom.)

Lower left: Enamel pattern of referred upper left second molar from Bloembosch, Darling. (After Haughton.)

Lower right: Original crown and sectioned enamel pattern of a broken, little worn, referred upper left fourth premolar from Wonderwerk. Sectioned surface approximately 2 cm. below crown. (From Cooke.)

All natural size.

very early wear but vanish rapidly with abrasion. The protocone is elongate oval in form, with rather more than one-third of its total length lying anterior to the junction with the protoconule. The range in size is, as far as observation goes, that deduced from the dimensions of the lowers.

Fig. 20 shows the form and pattern of the neotype (previously the type of *E. cawoodi*), the two teeth referred to the species by Broom (1913), that referred to it by Haughton (1932), and the sectioned damaged tooth from Wonderwerk. Fig. 21 gives the pattern of part of a series from Wonderwerk, two teeth from Floris Bad and one from the Vaal River gravels. These figures give a good idea of the characters and variations of the species.

The series of milk molars and two molars described by van Hoepen (1930 *a*) as *Equus gigas* do not appear to warrant specific distinction and may be referred to *E. capensis*. The upper teeth from Vlakkraal agree with those from Floris Bad to which Dreyer gave the name *E. helmei*, a species which Haughton (1932) regarded as a synonym of *E. cawoodi*. This is accordingly a synonym of *E. capensis*, as also is *E. westphali*, which Dreyer erected on lower teeth of large size from the Vaal River gravels at Pniel.

The tooth which van Hoepen (1930 *a*) referred to *E. cawoodi* and subsequently (1930 *b*) to a new species *E. louwi* does not appear to be *E. capensis*, but rather *E. kuhni* Broom. The same incorrect identification appears to apply to Dreyer's *E. cawoodi* (1931) and to the specimen described and wrongly figured by Broom and le Riche (1937). The smaller of the two right lower fourth premolars referred by the present writer (Cooke 1939) to *E. capensis* seems in the light of later knowledge to belong to *E. harrisi* Broom.

Equus kuhni Broom.

Equus kuhni Broom 1928. Ann. S. Afr. Mus., xxii, p. 444, fig. 3, B.
Equus cawoodi van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 1, pp. 3–4, fig. 2.
Equus louwi van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 2, pp. 19–21, figs. 6–11.
Equus kuhni Haughton 1932. Ann. S. Afr. Mus., xxviii, p. 414.
Equus kuhni Cooke 1941. S. Afr. J. Sci., xxxvii, pp. 307–308, fig. 3.
Equus capensis Broom and Le Riche 1937. S. Afr. J. Sci., xxxiii, pp. 769–770, fig. 1, A.

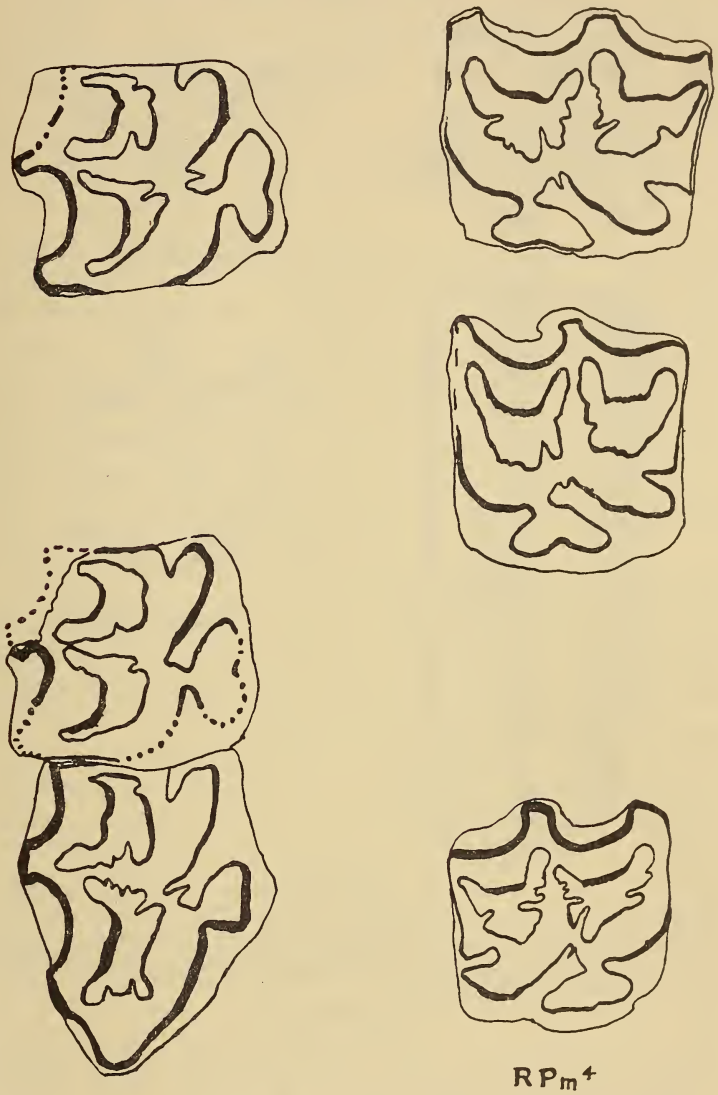


Fig. 21.—*Equus capensis* Broom.

Left: Part of incomplete series of referred left upper cheek teeth from Wonderwerk Cave. (From Cooke.)

Top right: Referred left upper fourth premolar and second molar from Florisbad. (After Dreyer.)

Lower right: Referred upper right fourth premolar from Vaal River gravels at Austin's Rush, Barkly West. (Original.)

All natural size.

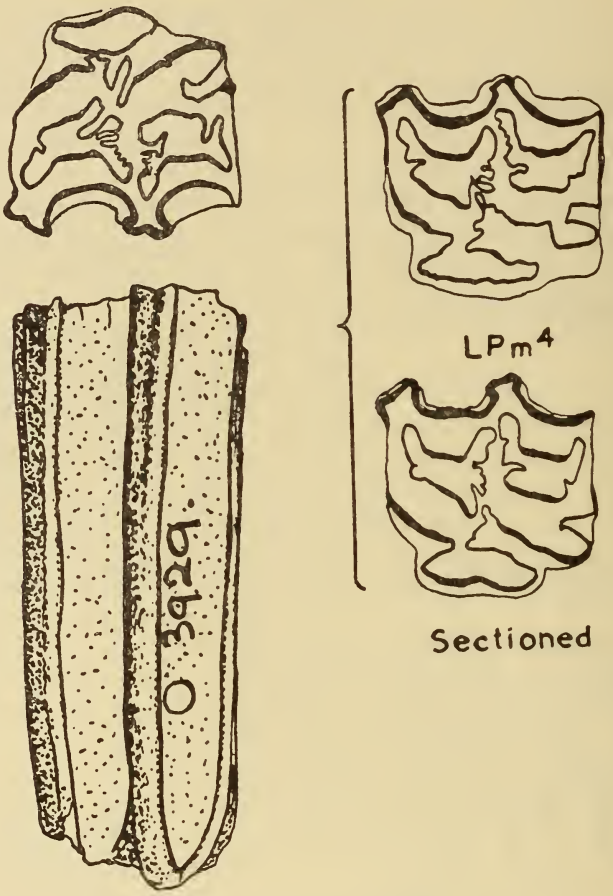


Fig. 22.—*Equus kuhni* Broom.
Left: Type upper right fourth premolar. (Original.)
Right: Neotype upper left fourth premolar from Wonderwerk Cave, showing pattern on little worn crown and on surface sectioned 2·5 cm. below the crown. (From Cooke.)
Natural size.

Type: Upper Pm⁴ of the right side. M.M.K., No. 3929. (Fig. 22.)
Locality: Pniel, Vaal River.
Horizon: ? Vaal River gravels.
Measurements:

	RPm⁴	2 cm. below crown
Breadth . . .	29·5 mm.	28·5 mm.
Length . . .	31·0 mm.	30·5 mm.
Height . . .	79·0 mm.	

Neotype: Upper Pm^4 of the left side. Arch. Sur., No. 143. (Fig. 22.)
Locality: Wonderwerk Cave, Kuruman District.
Horizon: Disturbed cave deposits.
Measurements:

	LPm^4	2·5 cm. below crown
Breadth . . .	27·5 mm.	28 mm.
Length . . .	29·5 mm.	28·5 mm.
Height . . .	77·0 mm.	

The type of this species, like that of *E. cawoodi*, is little worn; indeed the specimen is so little abraded that the protocone is not yet properly connected to the protoconule. The pattern it presents is thus not typical, and it has been necessary to create a neotype which has been sectioned to show the simplified pattern consequent upon more advanced wear. The marked grooving of the mesostyle does not extend far down the tooth. It is also apparent in the type that the smooth and deep concavity of the two halves of the ectoloph is a feature of the early state of attrition and that further wear would show these to be a little more flattened.

The upper teeth are intermediate in size between those of *E. capensis* and *E. quagga**, the breadth in Pm^3–Pm^4 being about 27–30 mm., and in M_1–M_2 about 26–29 mm. The halves of the ectoloph are concave with a slight flattening of the inner face, and the parastyle and mesostyle are prominent and somewhat abruptly marked off as in *E. zebra**. The anterior face of the parastyle is obliquely flattened and commonly slightly grooved in the premolars. The protocone is elongate oval with a flattened or a "bilobed" inner wall. Its junction with the protoconule is not much in front of the middle of the protocone. The hypocone is small and has the appearance of a tendency towards isolation, as the hypoglyph is unusually deep in many specimens and there is also commonly an indentation in the wall of the medivallum between the hypocone and the metaconule. The caballine fold is usually present and may be quite strongly developed. The pli-protoconule is well developed and often deep, as also is the pli-postfossette. The pli-postfossette is usually clearly shown and secondary plications are common. The pli-hypostyle and pli-protoloph are very variable in development and the former is sometimes well marked.

The lower teeth are not certainly known, but from the normal size relationship between upper and lower teeth they should range from 16·5 to 19 mm. for Pm^3 to Pm^4 and 15·5 to 18 mm. for M^1 to M^2. The species, *E. harrisi* Broom lies in the correct size group, and there is a

strong probability that *E. kuhni* is the upper dentition of that species.

In 1937 Broom and le Riche described and figured certain teeth which they referred to *E. capensis*. The Bothaville material has not been seen by the present writer, but the Sterkfontein specimens were amongst those lent to him by Broom. The lower jaw described by Broom and le Riche from Sterkfontein have the incisors and a second premolar present, and in size these exceed those of the living horses, but are otherwise not specifically identifiable. They might belong to *E. capensis*, *E. kuhni*, *E. harrisi* or *E. plicatus*. The upper palate and teeth from Sterkfontein were not found in association with the lower jaw.

This upper jaw is well embedded in the typical rather hard cave matrix, and it has proved impossible to clean the specimen properly in the normal manner. The occlusal surface of some of these teeth had been ground down by Broom to expose the enamel pattern, and the pattern of the first right molar was figured in the paper cited (fig. 1, A, p. 770) and measurements given. When the present writer examined the material, however, it was realised that the ground surface was very oblique to the plane of normal wear with a consequent distortion and exaggeration of breadth. The whole specimen was accordingly carefully ground down parallel to the palate and the dentition exposed as it would appear in early wear. The surface of the specimen (Tvl. Mus., No. 682) with the patterns now exposed is shown, natural size, in fig. 24. The dimensions are:

	RPm^2	RPm^3	RPm^4	RM^1	RM^2	RM^3
Breadth .	29·0 mm.	? 29 mm.	? 30 mm.	27·5 mm.	? 27 mm.	? 26 mm.
Length .	36·5 mm.	29·5 mm.	30 mm.	30·5 mm.	29·5 mm.	? 28 mm.

The whole character of the teeth places the specimen in the species *E. kuhni*, of which it is an excellent example.

The molar originally referred by van Hoepen (1930 *a*) to *E. cawoodi*, and later (1930 *b*) cited as the type of a new species *E. louwi*, is a very typical tooth of *E. kuhni*, as also are the other teeth ascribed to *E. louwi*. Haughton (1932) has already suggested that this species is a synonym of *E. kuhni*, and this view is confirmed.

The teeth which Dreyer (1931) refers to as "*Equus kuhni simplex*" are difficult to refer with certainty, but the "wholly unfossilised fourth premolar dug up at Glen Craig, Grahamstown", looks remarkably like *E. zebra**, while the one from Pniel is too small to be *E. kuhni* and agrees excellently with little worn teeth of *E. burchellii**. The partly fossilised first and second molars "dug up by Mr. S.

FIG. 23.—*Equus kuhni* Broom.
Palatal view of referred specimen from Sterkfontein Cave, embedded in matrix and with enamel patterns of upper cheek teeth exposed by grinding and polishing the rock. Natural size. (Original.)

Kinneard in Grahamstown", however, agree excellently both in size and character with *E. kuhni* and may certainly be assigned to that species.

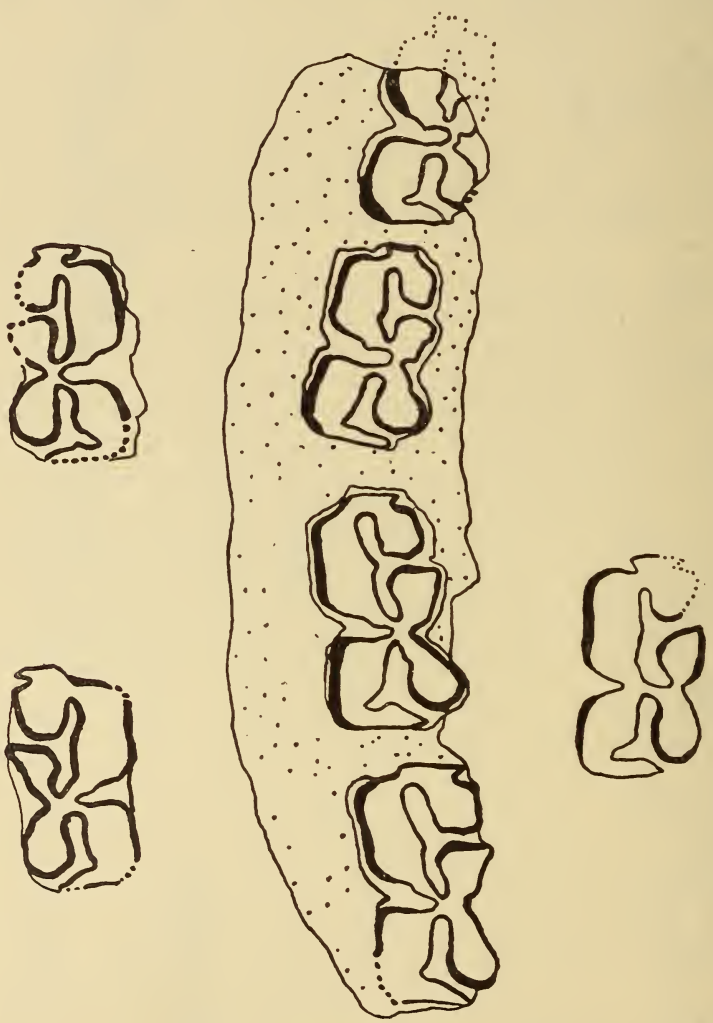


Fig. 24.—*Equus harrisi* Broom.

Top: Type left lower second molar and fourth premolar. (Original.)
Centre: Referred right lower cheek teeth from Sterktontein Cave. (Original.)
Below: Referred right lower fourth premolar from the Vaal River gravels at Pniel. (From Cooke.)

All natural size.

Equus harrisi Broom.

Equus harrisi Broom 1928. Ann. S. Afr. Mus., xxii, pp. 441, fig. 2, B.

Equus (*Sterrohippus*) *harrisi* (pars) Haughton 1932. Ann. S. Afr. Mus., xxviii, pp. 412–413.

Equus capensis (pars) Cooke 1939. S. Afr. J. Sci., xxxvi, p. 413, fig. 2, A.

(non *Equus harrisi* Dreyer 1931. "New Fossil Mammals and Man", pp. 23–25, pl. vi, figs. 13, 14; pl. vii, figs. 11, 12.)

Lectotypes: Left lower M_2 and Pm_4. M.M.K., No. 3939. (Fig. 24.)

Locality and *Horizon*: "Diamond gravels of the Middle Terrace at the bend near Barkly West."

Measurements:

	LM_2	LPm_4
Breadth	16·5 mm.	17·5 mm.
Length	29·5 mm.	30·5 mm.
Height (excluding roots)	37·0 mm.	45·0 mm.

The species is a good deal larger than *E. burchellii**, which it somewhat resembles, and it is smaller than *E. capensis*. The type specimens are very much worn, and this fact makes specific identification with less worn specimens rather difficult.

A feature of the species is its relatively greater antero-posterior compression compared with corresponding teeth in *E. capensis*. In the premolars, the entoflexid lobe is simpler and smaller than in *E. capensis*. There is also a marked tendency in the premolars for the indentation between hypoconid and hypolophid to be very small or absent. The outer walls of the well-developed hypoconid and protoconid are flattened or even slightly concave inwards, the ectostylid fold in the hypoconid wall being small or lacking. There is a strongly developed entaconid of rounded or quadrate form. The metaconid is relatively large and elongate antero-posteriorly, while the metastylid is smaller and pear-shaped. The valley between metaconid and metastylid is bluntly pointed.

Good material of this species is difficult to find, but an excellent series discovered by Broom in the hard limestone of the famous Sterkfontein Cave was given to the writer for identification and is figured here (fig. 24) for the first time.* It is unfortunately impossible to remove these teeth from their matrix, but the available dimensions are:

	RPm_3	RPm_4	RM_1	RM_2
Breadth	17·5 mm.	18 mm.	16·5 mm.	16 mm.
Length	33·0 mm.	32 mm.	28·5 mm.	? 28 mm.

* Also see Appendix.

A lower right fourth premolar from Pniel was identified and figured in error by the present writer (Cooke, 1939, p. 413, fig. 2) as belonging to *E. capensis*. This tooth (Arch. Sur., No. 5) is now assigned to *E. harrisi* and is refigured here. Its breadth is 17 mm., its length 30·5 mm. and its height 74 mm.

The lower right fourth premolar (M.M.K., No. 4066), figured by Haughton (1932, p. 415, fig. 3, B) and referred by him to *E. simplex* van Hoepen, probably belongs to this species, as also may the associated right first molar (M.M.K., 4047).

Referred Upper Teeth.

In his original paper Broom (1928) refers to this species a right upper Pm^4 from the same locality. Considering the nature of this deposit, the fact of an associated occurrence is only of very slight value in connecting the specimens. On a basis of size relationship between upper and lower teeth, the upper Pm^4 corresponding to the type lower tooth of this species should be about 28 or 29 mm. broad. The associated specimen referred by Broom has a transverse diameter of 31 mm. which, though not certainly outside the possible range, is rather on the large size. In view of these considerations the reference of this upper tooth to *E. harrisi* cannot be regarded as satisfactory, and the tooth is therefore provisionally made the type of a new species *Equus broomi* described below.

Van Hoepen (1930 *a*) referred this specimen to a new genus and species *Sterrohippus robustus* which he created on a second premolar. A second premolar cannot be regarded as forming adequate material for the type of a species, nor does there appear to be grounds for separating the genus from *Equus*. His specific name could not be retained as a species of this latter genus, as it is preoccupied by *Equus robustus* from the Pleistocene of Europe. *Sterrohippus robustus* is therefore regarded as incorrectly founded and invalid.

The upper teeth of *Equus harrisi* must for the moment be regarded as unknown until they are found in a good association with recognisable lower teeth. The rather poor lower teeth found in apparent association with upper teeth assigned to *Equus kuhni* Broom agree fairly well with those of *E. harrisi*, but there is as yet insufficient material to warrant identification with that species. The upper teeth of *E. kuhni*, however, are in precisely the right size group and it is very possible that *E. kuhni* represents the upper dentition of *E. harrisi*. The association of the two species in the Sterkfontein group of caves may also be significant.

Equus plicatus (van Hoepen).

Kolpohippus plicatus van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 1, pp. 8–10, fig. 10.

Equus plicatus Dreyer 1931. "New Fossil Mammals and Man", pp. 33–35.

Equus plicatus Haughton 1932. Ann. S. Afr. Mus., xxviii, p. 417.

Type: Lower series Pm_2 to M_1 of the right side. Nas. Mus., No. C.425. (Fig. 25.)

Locality: Tierfontein, near Port Allan, O.F.S.

Horizon: Not given in description; probably surface deposits.

Measurements: The measurements cited in the type description do not agree with the text-figure, but it appears that the breadths given are total breadths and not just the width across the enamel. The dimensions given below give the breadth over the enamel, estimated by enlarging the illustration in van Hoepen's paper to agree as well as possible with the various measurements he cites. The text-figure of the type series given here is the one derived in this way:

	RPm_2	RPm_3	RPm_4	RM_1
Breadth . .	17·5 mm.	17·5 mm.	15+ mm.	15·5 mm.
Length . .	38·0 mm.	33·0 mm.	30 mm.	27·0 mm.
Height . .	68·0 mm.	81·0 mm.	89 mm.	79·0 mm.

\+ very little worn.

The lower teeth are larger than those of *E. quagga** and smaller than those of *E. capensis*, agreeing in size with those of *E. harrisi*, which they otherwise closely resemble. The probable range of breadth in Pm_3 to Pm_4 is about 15·5 to 19 mm., and in M_1 to M_2 14·5 to 17·5 mm. The outer walls of the protoconid and hypoconid are flattened or even concave inwards in the premolars; in the molars the protoconid may be convex. A strong ectostylid fold is present in the anterior part of the hypoconid wall in the premolars, but this fold is small or even absent in molars. The metaconid is rounded, and is separated from the bluntly pointed metastylid by a pointed groove. The entaconid is quadrate and smaller than the metaconid. The lobe of the entoflexid is complicated in the premolars by strong—or at least well-marked—crimping of the inner wall of the hypoconid. The molars are much simpler than the premolars and cannot be easily distinguished from those of *E. harrisi*.

Van Hoepen's reference of the type teeth to a new genus does not

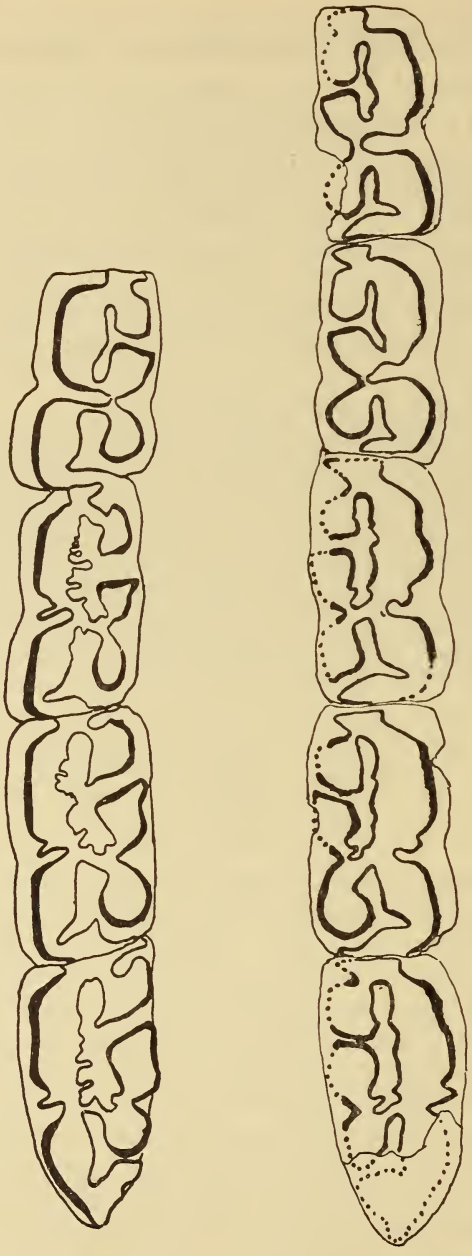


Fig. 25.—*Equus plicatus* (van Hoepen).

Left: Crown view of type series of right lower cheek teeth. (After van Hoepen; modified.)

Right: Crown view of series of lower left cheek teeth from damaged lower jaw from Koffiefontein, Orange Free State. This jaw is shown at the bottom of fig. 6. (Original.)

Natural size.

appear justifiable and even if the species is valid, it must be placed in *Equus*.

A fine series of teeth in a damaged left lower jaw from Koffiefontein, O.F.S., may be referred to this species with considerable certainty. The jaw (M.M.K., No. 4345) is shown in fig. 6 in comparison with a skull of *E. burchellii** and the enamel pattern of the teeth is shown in fig. 25. The inner side of the dentition is slightly damaged but the dimensions over the enamel are given below:

	LPm_2	LPm_3	LPm_4	LM_1	LM_2
Breadth . .	17 mm.	17·5 mm.	17·5 mm.	16·5 mm.	15·5 mm.
Length . .	38 mm.	33 mm.	33 mm.	29 mm.	29 mm.

It would appear very probable that the differences between the dentitions ascribed to *E. harrisi* and to *E. plicatus* are not really of specific value. The type teeth of *E. harrisi* are very worn indeed, and it is difficult to assess the probable appearance of the teeth of this species in early wear. There can, however, be little doubt that teeth of *E. plicatus* in advanced wear would be indistinguishable from those assigned to *E. harrisi*.

The upper teeth are not known from a certain association. There is a strong probability that the upper dentition of a skull from the same locality (Koffiefontein) as the lower jaw described above may be that of *E. plicatus*. This upper dentition has been described by Wells as *E. fowleri*, and in the absence of a certain association the merging of these two species must remain an open question.

Equus fowleri Wells.

Equus fowleri Wells 1941. Trans. Roy. Soc. S. Afr., xxviii, pp. 301–306, fig. 1, pl. lv.

Cotypes: "Portions of skull and isolated tooth catalogued as No. 555 in the collection of the Department of Anatomy, University of the Witwatersrand, Johannesburg." (Figs. 6 and 26, A. B.)

Locality: Koffiefontein, O.F.S.

Horizon: "At a depth of about 18 inches in surface soil overlying shale."

Material: This comprises "the greater part of the right maxilla and palatine bone with Pm^2–M^3 in position and perfectly preserved, the right maxilla containing an unerupted I^3 and part of the left maxilla lacking teeth". "The presence of the socket for C suggests that the individual is a male." "The remains are those of an individual not quite fully grown."

FIG. 26.—*Equus fowleri Wells.*

A. Crown pattern of right upper cheek teeth of type.
B. Crown pattern of cotype left upper first molar from the type locality.
C. Enamel pattern on sectioned surface 15–20 mm. below crown of cotype Lm^1 shown in B.
D. Crown pattern of referred upper right second molar.

All natural size. (From Wells.)

Measurements:

Skull: Length of upper jaw . . . . . About 44·5 cm.
Breadth across the first molars . . . . . 16·5 cm.
Length of Pm^2–M^3 . . . . . 20·6 cm.
Diastema between Pm^2 and I^3 . Approximately 11 cm.

Teeth:

	Pm^2	Pm^3	Pm^4	M^1	M^2	M^2
Breadth . . .	29 mm.	31 mm.	31 mm.	30 mm.	29 mm.	24 mm.
Length . . .	44 mm.	35 mm.	32 mm.	32 mm.	33 mm.	32 mm.
Length of protocone	13 mm.	14·5 mm.	15 mm.	13·5 mm.	15 mm.	15 mm.
Height (ex. roots) .	56 mm.	66 mm.	70 mm.	64 mm.	74 mm.	76 mm.

The following account is based on the type description, much being directly or indirectly quoted from Wells' paper.

The dimensions of the skull exceed those of many specimens of *E. caballus** and considerably exceed those of the zebrine horses. The lateral aspect of the maxilla in its upper portion, below the naso-maxillary suture, shows a marked hollowing. This region thus presented a form seen in the asses and in the quagga group, but not in the caballine horses nor, to any marked degree, in the mountain zebra.

The teeth are large, being intermediate in size between those of *E. capensis* (*E. cawoodi*) and *E. kuhni*, both of which they somewhat resemble. The halves of the ectoloph are deeply concave inwards, and curve rather sharply into the styles with a tendency for the mesostyle to overhang anteriorly. Both parastyle and mesostyle are prominent and massive, especially in the premolars, and are more or less conspicuously grooved. The protocone is elongate, and its connection with the protoloph is established very near its anterior extremity, so that the elongation appears to affect chiefly the posterior lobe. The medial wall of the protocone is sinuous, with an ill-defined median groove. In Pm^3 and Pm^4 the protocone has a remarkably oblique direction, and these two teeth in the type show an unusual prominence of the hypostyle.* The caballine fold is well developed and may be duplicated. The enamel of the fossettes is irregularly crimped and its secondary plications are numerous but relatively coarse. The pli-protoloph and pli-hypostyle are well developed in early wear. The pli-protoconule is unusually complex and even in M^1 is duplicated. The pli-postfossette is also rather complex, but the pli-prefossette is simpler, though small secondary folding may be present.

Another tooth found half a mile distant from the skull fragments at a depth of five feet in similar soil has been referred to this species.

* This is almost certainly a feature of early wear.

It is an upper left first molar and shows all the characteristics of the type, but is from a different individual, also young. The measurements of this tooth are:

Breadth	30 mm.
Length	32 mm.
Height (excluding roots)	65 mm.

The pattern it presents is a little more complex in its secondary plication than that of the type (fig. 26, B). A section has been made through the tooth 15–20 mm. below the grinding surface, where the pattern is somewhat simplified but remains essentially the same (fig. 26, C.)

In the McGregor Museum there occurs a right upper M^2 (M.M.K., 4342) also from Koffiefontein which Wells refers to his species (fig. 26, D). It is more worn than the corresponding tooth of the type and is a little smaller, its dimensions being:

Breadth	28·5 mm.
Length	29·5 mm.
Height (excluding roots)	76 mm.

The styles are narrower than in the type and are very indistinctly grooved, and the pli-hypostyle is single though remarkably large. These differences, however, are not outside the expected range of variation of such a species and the tooth is referred to *E. fowleri.*

As has been stated above, the lower jaw which agrees so well with the type of van Hoepen's *E. plicatus*, was found also at Koffiefontein, and this dentition is of a suitable size to correspond with *E. fowleri.* There is thus a good possibility that these names are synonymous, but such a decision must await confirmation from a better association.

It also seems very likely that *E. fowleri* is merely a somewhat abnormal variant of *E. kuhni*, and that, in fact, *E. kuhni*, *E. harrisi*, *E. plicatus* and *E. fowleri* represent only a single species.*

Equus sandwithi Haughton.

Equus sandwithi Haughton 1932. Ann. S. Afr. Mus., xxviii, pp. 419–421, fig. 4.

Cotypes: Upper right Pm^2 and Pm^3 and incomplete M^3.
Upper left Pm^5 and Pm^4.
Lower right M_1 and incomplete Pm_3.
Lower left M_1 and M_2.
S.A. Mus., Nos. 6577 and 6578. (Fig. 27.)

Locality: Usakos, South-West Africa.

* Also see Appendix.

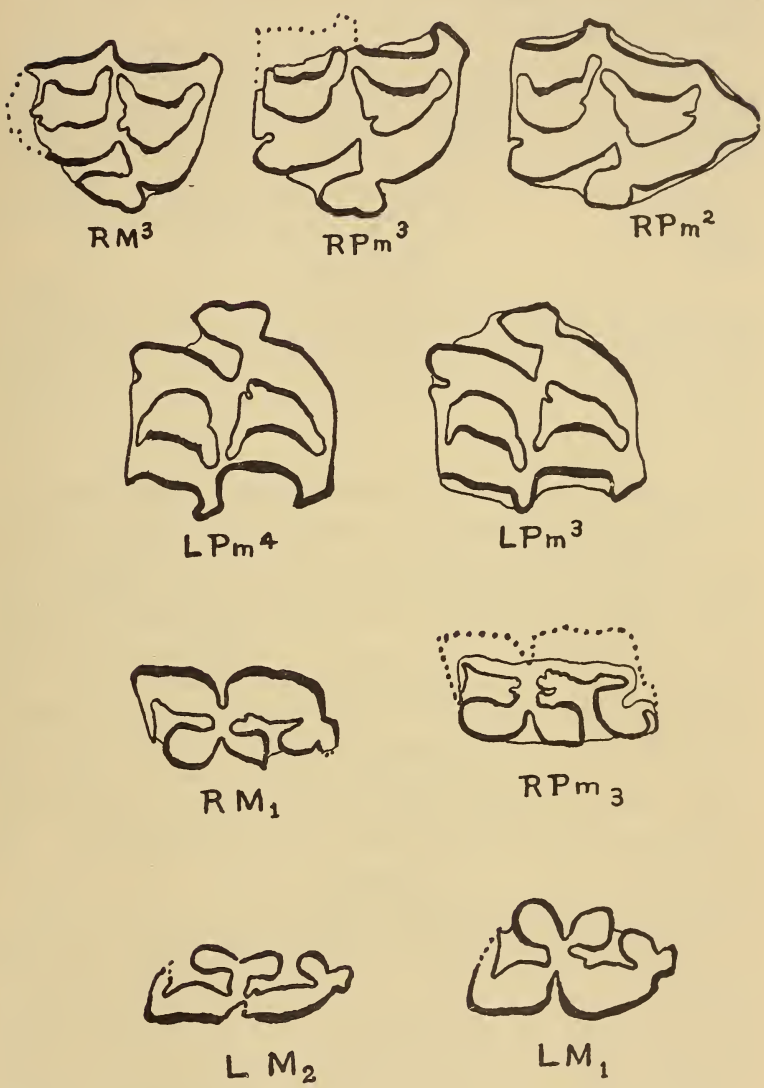


FIG. 27.—*Equus sandwithi* Haughton. Cotype upper and lower cheek teeth. Natural size. (Original.)

Horizon: In a bed of hard clay and sand 10 feet thick underlying 8 feet of surface limestone.

Measurements:

Upper	RPm^2	RPm^3	RM^3	RPm^3	LPm^4
Breadth	26·5 mm.	28 (?) mm.	24·5 mm.	29 mm.	32 mm.
Length	35 mm.	28·5 mm.	29 (?) mm.	29 mm.	29 mm.
Height (ex. roots)	56 mm.	54 mm.	67 mm.	53 mm.	57 mm.
Length of protocone	7 mm.	10·5 mm.	11 mm.	9 mm.	10 mm.

Lower	RPm_3	RM_1	LM_1	LM_2
Breadth (Est.)	16–17 mm.	15 mm.	16 mm.	11·5 mm. (14·5)
Length	30 mm.	29·5 mm.	29 mm.	29 mm.
Height (ex. roots)	70 mm.	78 mm.	65 mm.	77 mm.

Haughton's measurements differ slightly from those given above, the explanation lying in the fact that the breadth quoted here is measured directly across the tooth and not along the rather sloping surface of wear. The tooth which Haughton describes as a lower left third molar is here regarded as a lower left second molar in very early wear. The very narrow enamel surface is a feature of early wear, and the crown is 3 mm. wider half an inch below its present surface.

The upper teeth of this species resemble those of *Equus zebra** but are a good deal larger and present an even simpler enamel pattern. The halves of the ectoloph are flattened or even bulge outwards near their centres. The parastyle and mesostyle are strongly developed and well demarcated. The mesostyle is rather narrow, and the parastyle has an oblique flattened face which may be grooved. The protocone is abnormally small, being proportionally even shorter than in *E. zebra**. This shortness is due to the very small development of the anterior prolongation. The fossettes are large and lunate. They are almost devoid of folding, only the pli-protoconule being distinct while the other folds are almost indistinguishable. The pli-caballin is absent. The hypoglyph is shallow. The protoconule shows marked antero-internal flattening.

The lower teeth are unusual in shape, as they present an anterior face which is oblique to the axis of the tooth instead of directly transverse to it. This is due to the posterior deflection of the point of the parastylid and its anterior face. The walls of the protoconid and hypoconid are rounded or slightly flattened and the ectostylid fold is inconspicuous or absent. The entaconid is moderately small in the molars. The metaconid and metastylid are normally large and pear-shaped, but their attitude may be distorted by the relative compression of the interior side of the tooth. The anterior part of the entoflexid tends to be slightly or moderately folded.

The ratio of size of molars and premolars is rather unusual, as the molars appear relatively to be abnormally small and narrow both in upper and lower dentitions. The type LPm^4 owes its unusual width at least in part to the abnormal projection of the mesostyle, but it appears that the expected range in breadth would be 28–33 mm. in Pm^3 and Pm^4 and 26–29 mm. in M^1 and M^2, with the anterior and posterior teeth notably narrower. The same applies to the lower teeth, in which the range in Pm$_3$ and Pm$_4$ may be 15–18 mm. and in M$_1$ and M$_2$ 13–17 mm.

Referred Material.

Haughton (1932) assigned to *E. sandwithi* two lower teeth from the Vaal River gravels at Sheppard Island. These teeth were discovered by van Riet Lowe but were lost in the library fire at the University of the Witwatersrand in 1931.

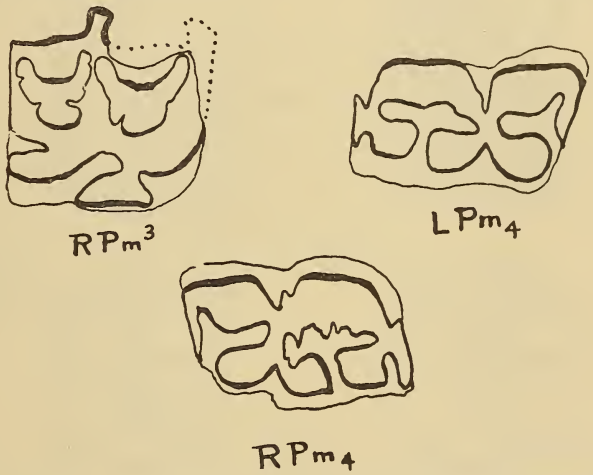


Fig. 28.—*Equus sandwithi* Haughton. Referred upper and lower cheek teeth from the Kromdraai Cave. Natural size. (Original.)

Amongst the material collected by Broom in the Kromdraai Cave deposit there occur several teeth which appear to belong to this species. Most of the teeth, both upper and lower, are damaged and difficult to clean, but a selection of the better ones is shown in fig. 28.

Equus poweri Cooke.

Equus poweri Cooke 1939. S. Afr. J. Sci., xxxvi, pp. 412–414, fig. 1.

Type: Upper right first molar. Arch. Sur., No. 3. (Fig. 29).
Locality: Pniel, Vaal River.
Horizon: ? Younger gravels of Vaal River.
Neotype: Upper left first molar. Arch. Sur., No. 213. (Fig. 29.)
Locality: 35-foot shaft, Lot 197, Windsorton.
Horizon: Younger gravels of Vaal River.

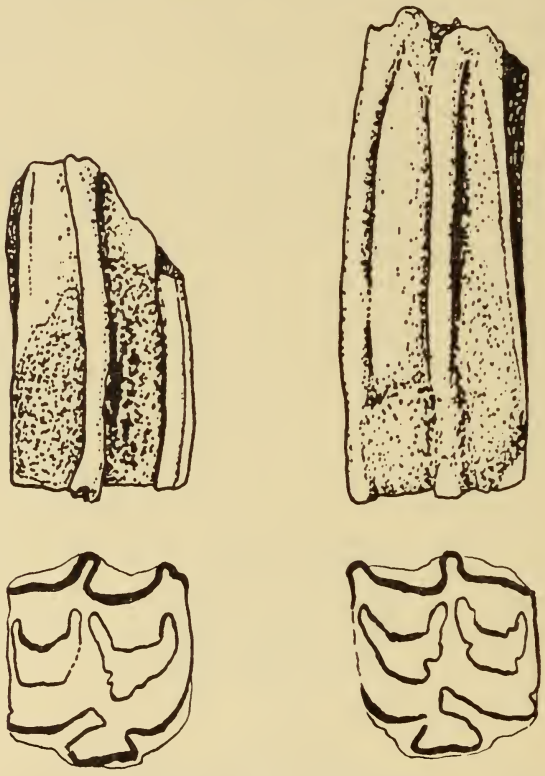


Fig. 29.—*Equus poweri* Cooke.
Left: Type right upper first molar. Outer and crown views.
Right: Neotype left upper first molar. Outer and crown views.
Natural size. (Original.)

Measurements:

	Type RM^1	Neotype LM^1
Breadth . . .	27 mm.	26 mm.
Length . . .	24 mm.	23 mm.
Height . . .	44 mm.	64 mm.

This species resembles *Equus sandwithi*, but appears to be very slightly smaller and to differ in several particulars. The halves of the

ectoloph are moderately flattened or bulge outwards near their centres, and the parastyle and mesostyle are well demarcated. Though prominent, the mesostyle is not nearly as well developed as in *E. sandwithi*. The protocone is very small, but the anterior lobe is proportionately larger than in *E. sandwithi* and more like *E. zebra** in this respect. The fossette are large and simple, the post-fossette being subrectangular in shape and not lunate as in *E. sandwithi*. The pli-protoconule is small and the hypostyle and protoloph folds are present only as small notches. The medivallum is small and narrow and devoid of any trace of a caballine fold. The protoconule shows a well-rounded antero-internal face and is not flattened as in *E. sandwithi*. The hypoglyph is very shallow and may disappear altogether towards the base of the tooth.

The estimated dimensions fall a millimetre below those of *E. sandwithi*.

Equus broomi sp. nov.

Equus harrisi (pars) Broom 1928. Ann. S. Afr. Mus., xxii, pp. 442–443, fig. 2 (B_3).

Type: Upper right fourth premolar. M.M.K., No. 3939 *c*. (Fig. 30.)

Locality: The Bend, near Barkly West.

Horizon: "Middle Terrace" of the Vall River gravels.

Measurements:

	RPm⁴
Breadth	31 mm.
Length	32 mm.
Height	62 mm.
Length of protocone	9 mm.

This tooth, which is badly battered, was assigned by Broom to the species *E. harrisi* on account of the association of the specimen with the two lower type teeth of that species. This association is not a good one in view of the very disturbed nature of the deposit, and the upper tooth seems somewhat large to be correctly associated with the lowers. It is therefore given a new name here until certain associations settle the problems of the relations between the various species named on upper and on lower teeth.

The resemblance of this species to *Equus sandwithi* is strong, almost the only marked difference, apart from the greater size, being the shape of the ectoloph, which is smoothly concave in both halves and is only slightly overhung by the parastyle. The protocone is very short and

unusually rounded. The hypocone projects into the medivallum as a slight bulge but the hypoglyph is small. The fossettes show more folding than is the case in *E. sandwithi*, the pli-protoloph, pli-postfossette and pli-protoconule being distinct though small, and

FIG. 30.—*Equus broomi* sp. nov. Outer lateral and crown views of the type upper right fourth premolar of *Equus broomi* sp. nov.; formerly referred to *Equus harrisi* Broom. Natural size. (Original.)

there is a certain amount of minor folding in the posterior wall of the prefossette.

The specimen on which van Hoepen created the new genus *Sterrohippus* and species *robustus* might belong to this species, but van Hoepen's specimen is a second premolar which cannot be regarded as forming adequate material for specific identification. There is no reason to support the generic status of *Sterrohippus*, which is indistinguishable from many species of *Equus*, and the specific name *Equus*

robustus is preoccupied and cannot be retained. *Sterrohippus robustus* is therefore regarded as invalid.

Incertae sedis.

Equus simplex van Hoepen 1930. Pal. Nav. Nas. Mus. Bloemfontein, II, 1, p. 5, fig. 6.

Type: Upper right first molar. (Nas. Mus., No. 284).
Locality: Koffiefontein, O.F.S.
Horizon: ? Surface.
Measurements:

	RM¹
Breadth . . .	30 mm.
Length . . .	29 mm.
Height . . .	89 mm.

The type specimen has not been seen by the writer, and it is not possible from the drawing to assign the tooth with certainty to any particular species. If the dimensions given in the text of the type description are correct, the tooth may belong to *E. capensis* as suggested by Haughton (1932). Otherwise from the text-figure it resembles *E. kuhni* more closely than *E. capensis*, so that the position (or the validity) of this species is uncertain.

Guide to Equine Species.

Incisors.

A. Very broad mandibular symphysis with large, anteriorly flattened first and second incisors and reduced third incisors. (Upper incisors unknown.)
Eurygnathohippus cornelianus v. Hoep.

B. Incisors of the normal (i.e. *Equus caballus**) type possessing the cup or "mark" in the upper jaw but lacking it in the lower jaw.
*Equus burchellii** (Gray).

C. Incisors of the "normal" type with the cup or "mark" present at least in the first and second incisors of both jaws.
? *Equus quagga** Gmelin.
*Equus zebra** Linn.
? *Equus capensis* Broom.
? *Equus kuhni* Broom.
? *Equus fowleri* Wells.

D. Incisors unknown.
Equus harrisi Broom.
Equus plicatus (v. Hoep.).
Equus sandwithi Htn.
Equus poweri Cooke.
Equus broomi Cooke.
(*Equus simplex* v. Hoep.)
Notohipparion namaquense Htn.
Stylohipparion steytleri (v. Hoep.).

Upper Cheek Teeth.

A. Protocone isolated; parastyle anteriorly flanged.
Stylohipparion steytleri (v. Hoep.).
(Pm. ? 19–24 mm. M. 18–23 mm.) *

B. Protocone attached.
1. Breadth less than 27 mm.
(*a*) Ectoloph halves concave; parastyle obliquely flattened anteriorly.
*Equus burchellii** (Gray).
(Pm. 22–26 mm. M. 21–25 mm.)
(*b*) Ectoloph halves flattened.
*Equus zebra** Linn.
(Pm. 22–27 mm. M. 21–26 mm.)
*Equus quagga** Gmelin.
(Pm. 22–27 mm. M. 21–26 mm.)

2. Breadth greater than 27 mm.
(*a*) Ectoloph halves concave; parastyle usually flattened.
Equus capensis Broom.
(Pm. 29–35 mm. M. 27–33 mm.)
Equus kuhni Broom.
(Pm. 27–30 mm. M. 26–29 mm.)
Equus broomi Cooke.
(Pm. 28–33 mm. M. 27–32 mm.).
Equus fowleri Wells.
(Pm. 29–33 mm. M. 28–32 mm.)
(*b*) Ectoloph halves flattened; parastyle prominent.
Some *E. kuhni* premolars.

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* These dimensions are range of breadth.

Equus sandwithi Htn.
(Pm. 28–33 mm. M. 26–29 mm.)
Equus poweri Cooke.
(Pm. ? 26–29 mm. M. 25–28 mm.)

C. Position uncertain.
Equus simplex v. Hoep.

D. Upper cheek teeth unknown.
Equus plicatus (v. Hoep.).
Equus harrisi Broom.
Notohipparion namaquense Htn.
Eurygnathohippus cornelianus v. Hoep.

Lower Cheek Teeth.

A. External ectostylid column present.
1. Strong protoconid fold or pillar; metaconid and metastylid strong.
Notohipparion namaquense Htn.
(Pm. 15–16 mm. M. 14–17 mm.)
2. Protoconid fold weak or lacking; metaconid and metastylid small.
Stylohipparion steytleri (v. Hoep.).
(Pm. 11–15 mm. M. 10–13 mm.)

B. No external ectostylid column.
1. Face of parastylid oblique; metaconid and metastylid strong.
Equus sandwithi Htn.
(Pm. 15–18 mm. M. 13–17 mm.)
2. Face of parastylid normal.
(*a*) Breadth less than 15 mm.
*Equus zebra** Linn.
(Pm. 12–15 mm. M. 11–14 mm.)
*Equus burchellii** (Gray).
(Pm. 12–15 mm. M. 11–14 mm.)
*Equus quagga** Gmelin.
(Pm. 12–15 mm. M. 11–14 mm.)
(Some molars of *E. plicatus* resemble *E. quagga**.)
(*b*) Breadth greater than 15 mm.
Equus harrisi Broom.
(Pm. 17–20 mm. M. 16–19 mm.)

Equus plicatus (v. Hoep.).
(Pm. 15·5–19 mm. M. 14·5–17·5 mm.).
Equus capensis Broom.
(Pm. 18·5–22 mm. M. 17·5–21 mm.)

C. Lower dentitions unknown.
Eurygnathohippus cornelianus v. Hoep.
Equus kuhni Broom.
Equus fowleri Wells.
Equus broomi Cooke.
Equus poweri Cooke.

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APPENDIX

(With Fig. 31.)

In the five years which have elapsed since this account of the Perissodactyla was written, certain additional information has come to light which, while it does not involve any important alteration of the views already expressed, nevertheless requires to be added in order to bring the work reasonably up to date.

Firstly, the description of the fossil mammals of the Vaal River deposits, mentioned in the Introduction to the present account, has appeared as Memoir 35 (III) of the Geological Survey of the Union of South Africa and it contains a certain amount of stratigraphic information on the distribution of the Equidae in those deposits (Cooke, 1949 *b*). In addition, revisions of the Suina (Cooke, 1949 *a*) and of the Proboscidea (Cooke, 1947) have been published as companion studies to the present one.

Secondly, a perissodactyl family new to this region has been recorded through the discovery of an undoubted Chalicothere in the cave breccia of the Makapan valley (George, 1950). The type is a left upper second molar and there are also a number of other cheek teeth and an ungual phalanx. The type molar and the phalanx are illustrated here (fig. 31). Chalicothere remains have previously been reported from the Kaiso beds of Uganda (Andrews, 1923) and from south Serengeti in Tanganyika (Dietrich, 1942), but the Makapan specimens appear distinct and were described as a new species tentatively placed in *Metaschizotherium* as *M. transvaalensis*. The resemblance to the Tanganyika species *M. hennigi* is fairly close and it is considered by Miss George that both species certainly belong to the same genus, whether or not this is really Metaschizotherium.

Thirdly, a new species of fossil equine has been erected by Broom (1948) based on material from a cave breccia in the Sterkfontein area about half a mile south-west of the site known as "Bolt's workings". The type of this species, *Equus zietsmani*, comprises an imperfect lower jaw with the incisors, most of the cheek teeth of the right side and some of those of the left side, and part of the left maxilla. The lower series from P_2 to M_2 can be well reconstructed and is figured by